Studies on the biology of moorland tipulidae with particular reference to molophilus ater meigen

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STUDIES ON THE BIOLOGY OF MOORLAND TIPULIDAE

WITH PARTICULAR REFERENCE TO *MOLOPHILUS ATER* MEIGEN

by

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..... being a thesis presented in candidature for the degree of Doctor of Philosophy in the University of Durham, 1971.

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ABSTRACT

Moorland Tipulidae (in particular, the brevi-palp crane-fly, Molophilus ater Meigen) have been studied on the Moor House Nature Reserve, Westmorland. Mean soil temperatures, which were measured by both mercury in steel thermographs and a chemical integration technique using sucrose solutions, showed a reduction of approximately 0.1°C for every 100' increase in altitude. Between site differences in temperature were about four times greater during the summer and autumn than they were during the winter and spring. The pattern of adult emergence for M.ater was obtained by using emergence traps and a vacuum sampler, and the mean date of emergence was approximately two weeks later at 2700' than at 1400'. The middle 68% of the emergence lasted about five days. Field experiments indicated that the site temperature during the spring determined the start of pupation and culture studies suggested a minimum threshold temperature for pupation of 5 to 6°C. This threshold is thought to be responsible for both the synchronising of the emergence and the delay in the emergence at higher altitudes. The densities of final instar larvae prior to pupation in the spring varied from approximately 700 to 2000 per sq.m. at different sites. An increase in the mean larval weight at any site, led to an increase in the mean weight of the subsequent female adults and to an increased fecundity, but the mean weight of the males was little changed. Key factor analysis has shown egg and first

instar mortality to account for most of the variation in generation mortality from year to year and this is thought to be due to desiccation. Another component within the egg and first instar mortality, thought to be due to predation, is shown, together with reduction in fecundity, to act in a density dependent manner and to contribute to the regulation of population numbers.

CONTENTS

1. INTRODUCTION

The work presented in this thesis, which has been carried out on the Moor House National Nature Reserve in Westmorland, has been largely concerned with one species of brevi-palp crane-fly, Molophilus ater Meigen, which was noted by Coulson (1959) to be an abundant insect at Moor House. The results of this work have been presented under three main headings, namely, the emergence biology of adult crane-flies at these sites, the population dynamics of M.ater, and a study of the temperature relations at the different sites. Cragg (1961) has summarised the many investigations into the biology of the soil fauna at Moor House, and Coulson (1956, 1959, 1962) has catalogued the crane-fly fauna of the reserve and investigated the biology of certain Tipula species.

The family Tipulidae can be divided into three sub-families (Coe 1951) of which the Tipulinae represent the long palped crane-flies, while the Cylindrotominae and Limoniinae comprise the short palped crane-flies. Most biological studies have concentrated on the Tipulinae. Barnes (1925, 1937) has considered aspects of the distribution and bionomics of Tipula paludosa Meig., Milne et al (1958) and Laughlin (1958, 1960, 1967) have contributed to the biology of Tipula oleracea L. and T.paludosa Meig., and Freeman (1964, 1967, 1968) has studied the population ecology of both larvae and adults. Freeman's last paper also included the brevi-palp group

as did the study by Crisp & Lloyd (1954) of the insects inhabiting a patch of woodland mud. Hadley (1966, 1969) has studied the biology of M.ater at Moor House.

Meteorological observations on the Nature Reserve were made by Manley (1936, 1942, 1943) but there have been few biological studies of the climate at higher altitudes. Millar (1964, 1965) has considered aspects of the climate of the Northern Pennines in relation to vegetation, and Healey (1967) has made an ecological study of the temperatures in a Welsh Moorland soil. It is in this context that the measurement of soil temperature has been extended to a variety of sites from 1200' to 2780' (366 to 847m) on Great Dun Fell, and of different vegetation but at the same altitude on the eastern side of the reserve.

There have also been few detailed studies on the progressive effect of the harsher environment at higher altitudes on the soil fauna. Jordan (1958, 1962) and Welch (1965) have studied the rush moth, Coleophora alticolella Zell., in this context, and Whittaker (1965) has considered the distribution and population dynamics of the Cercopids Neophilaenus lineatus L. and N.exclamationis L., partly in relation to altitude.
In the present study the access road to the radio station on the summit of Great Dun Fell, facilitated the field work concerned with the emergence pattern and life cycle of species living at six different altitude sites from 1400' to 2700' (427 to 823m).

A characteristic of M.ater is that in the adult stage both sexes are sub-apterous and their inability to fly has made the estimation of adult density much easier. The population studies started by Hadley (1966) have been continued in the present work, and the use of two of Hadley's study sites at Moor House, together with his measurements of population density, has allowed information on the density changes over the period 1963 to 1970 to be analysed in section five of this work, where the key factor methods of Morris (1959) and Varley & Gradwell (1960, 1963a, 1963b, 1965, 1968; and Varley 1963) have been employed.

Cragg (1961), summarising the ecological studies that have taken place at Moor House, particularly in the context of the Nicholson (1954a, 1945b, 1957, 1958) - Andrewartha & Birch (1954) controversy over population control, suggested that the marked variations in abundance that had been shown to occur, for example, by Coulson (loc.cit.) in T.subnodicornis Zetterstedt and Jordan (loc.cit.) in Coleophora alticolella, were due to two factors, the variability of the moorland habitat, and the violent fluctuations of a harsh climate. In such a situation, where the extinction of local populations was known to occur, he thought that regulation, implying the restricted fluctuation of numbers from adult generation to adult generation might be of little significance, and that it was the state of the species over the whole range of its possible habitats which was important in providing some overall stability.

The studies at the different altitudes on Great Dun Fell are important in this context, in that they can provide an indication of how severe the climate is for M.ater, since if the species is either directly or indirectly under pressure from the climate, it would be expected to manifest itself as greater mortality or reduced size at the higher altitude sites.

As it was noted above, Cragg (loc.cit.) also stressed the importance of habitat variation at Moor House, and he quoted as an example the work of Coulson (loc.cit.) who found that populations of T.subnodicornis were most abundant on Juncus squarrosus moor, but were made extinct in this habitat in one season by a severe drought during the egg and first instar stages in June and July. The population densities on an area of Sphagnum bog, which were normally much less than those on the J.squarrosus moor, showed no such decline. Coulson concluded that the wet Sphagnum habitat, albeit of low density, was important in the maintenance of the species by compensating for its disappearance elsewhere, and Cragg commented that "a species not too specific in its larval requirements has a better chance of survival under the markedly fluctuating conditions associated with high moorlands."

Hadley (1966) has considered the distribution of M.ater larvae, and found considerable differences in larval densities at different vegetation sites at Moor House. The highest densities, up to 2000 final instar larvae per sq.m, were found on peaty areas dominated by

J.squarrosus or Carex spp., and the lowest, approximately 150 per sq.m, on Blanket Bog. A site dominated by Eriophorum vaginatum had a density of 1040 final instar larvae per sq.m, while no larvae were extracted from soil samples taken from limestone grassland areas dominated by Festuca spp. and Agrostis spp., from bare peat areas, or from well leached mineral soils or redistributed peat areas dominated by Nardus stricta.

This may represent a preference for wetter peaty areas, with the exception of the sterile and unstable bare peat situations, or it may be that only the peaty sites provide certain strains of bacteria, fungi, and protozoa that are essential food for M.ater. Probably both these factors are important but in the absence of knowledge about what precisely constitutes the food of M.ater, the question has to remain open.

Note :

1. The species nomenclature for plants mentioned in this thesis is from

   Flowering plants - Clapham et al (1962)

   Mosses - Watson (1955)

2. The statistical analyses have been based on Bailey (1959) and the following symbols have been used

   d - a normal variable, with zero mean and unit standard deviation (p.36)

   t - the "Student's" statistic modified for small samples (p.48).

2. THE STUDY AREA AND SAMPLING SITES

2.1 Location and General Physiography

The Moor House National Nature Reserve (N.R.80, Nat.Grid Ref. NY/759329) occupies 4000 hectares (10,000 acres) of typical Pennine moorland in the county of Westmorland. The reserve lies 12 miles to the east of Penrith, and 11 miles to the south of Alston. The greater part of the reserve comprises the eastern, dip, slope from the summit ridge of the Pennines, and its boundary is formed to the north and east by the River Tees. The summit ridge of the reserve includes three principal fells, Knock Fell (2604', 794m), Great Dun Fell (2780', 845m), and Little Dun Fell (2761', 842m), while Cross Fell (2930', 893m), the highest peak of the Pennines, lies just outside the northern boundary. To the west of the summit ridge the scarp slope descends to the Vale of Eden, and the reserve boundary is provided by the upper limit of enclosed pasture, which is at about 1400' (427m).

The dip slope has an extensive cover of glacial drift, overlaid by peat, which reaches a depth of 12 feet in places. This is covered by blanket bog, except where there is dissection by the numerous streams which flow to the Tees, exposing the bed rock of the Carboniferous Yoredale Series and producing peaty or mineral soils, supporting a vegetation dominated by rushes and grasses.

Above about 2500' (762m) on the eastern slope, and on the western, scarp, slope, the peat has been mostly eroded to produce thin, fell top, podsol soils, dominated by Festuca spp. on the summits, and a variety of peaty and mineral soils on the western slope dominated by Festuca spp., Nardus stricta, or Juncus squarrosus.

General descriptions of the reserve have been given by Conway (1955) and Cragg (1961). The geology has been described in a monograph by Johnson & Dunham (1963) and the vegetation by Eddy, Welch & Rawes (1969).

2.2 The Study Sites

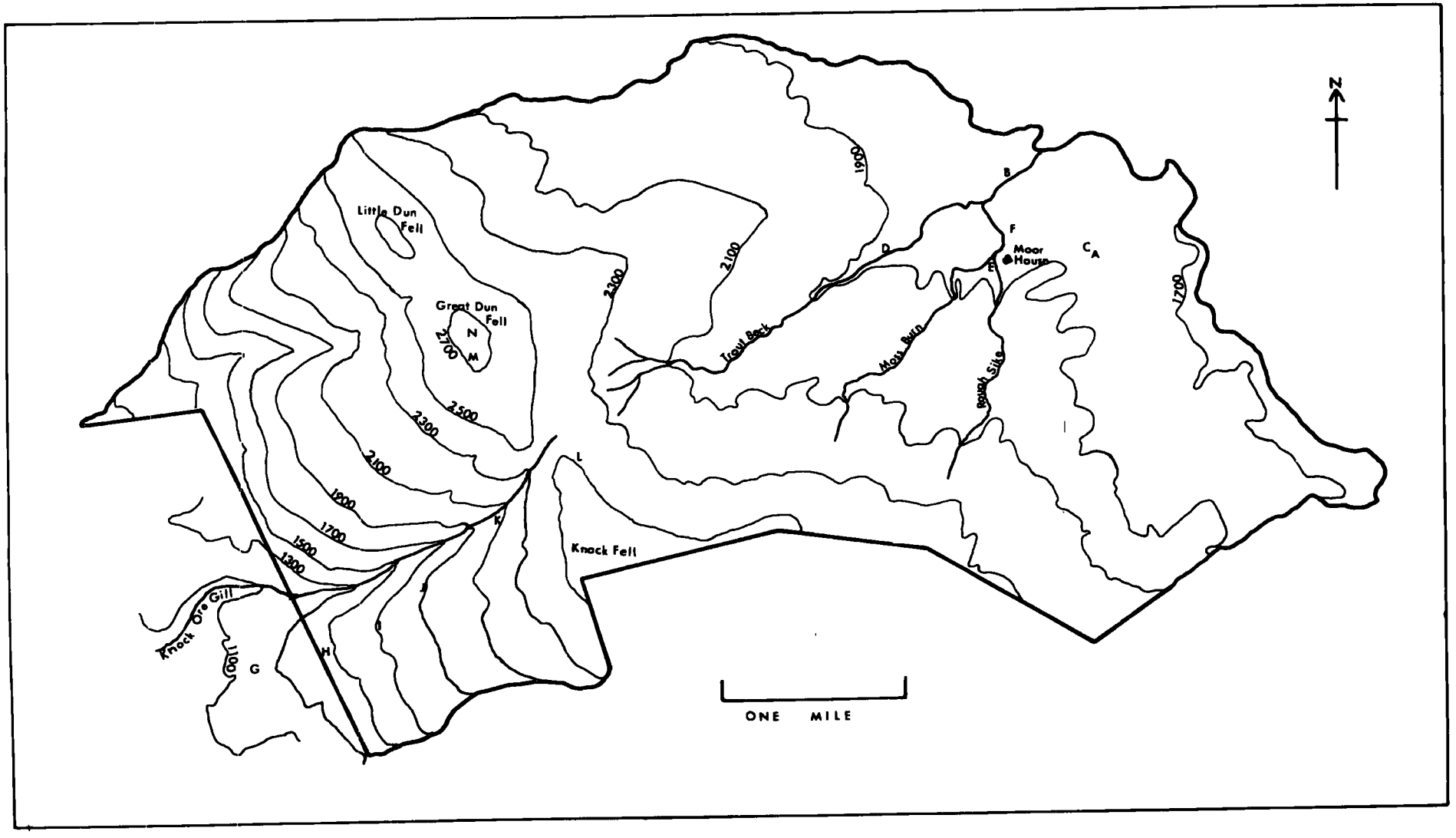
The study sites can be divided into two main groups; those on the eastern side of the summit ridge and all at approximately 1800' (549m) altitude, and those on the western, scarp, slope at different altitudes. The former have been referred to collectively in this thesis as the Moor House sites, as they were all within a mile of the house itself, and the latter have been collectively referred to as the Dun Fell sites.

The Moor House Sites

The six sites in this group included four sites previously used and described by Hadley (1966) and two others used by Coulson (1956).
The first four sites were used in the study of M.ater.

Map of the Moor House National Nature Reserve to show the location of the study sites.

Moor House Sites		Dun Fell Sites	
A	Peaty Gley	G	1200'
B	Peaty Podsol	H	1400'
C	Blanket Bog	I	1700'
D	Carecetum	J	1900'
E	Limestone Grassland	K	2050'
F	Above Netherhearth	L	2500'
		M	2700'
		N	2780'


N
Little Dun Fell
Great Dun Fell
Knock Fell
Moor House
Trout Beck
Moss Burn
Knock Ore Gill
ONE MILE
1900
2100
2300
2500
2700
1700
1500
1300
1100
A
B
C
D
F
G
H
L
M
N

1. Peaty Gley Site (1800', 549m)

This was a level, slightly flushed site, dominated by J.squarrosus, at the end of the track to Bog End. Between the Juncus rosettes there were clumps of Carex spp., Deschampsia flexuosa, and Festuca ovina. Herbs and lichens were rare, but the site supported a rich variety of bryophytes.

2. Peaty Podsol Site (1820', 555m)

On this site the mineral soil was covered by only a thin layer of peat, varying between 8 and 20cm deep. There was a SSE slope of approximately 7^{o}. J.squarrosus was again dominant and the site was characterised by the presence of Nardus stricta, indicative of the drier, more mineral substrate.

3. Blanket Bog Site (1840', 561m)

Blanket Bog comprises the major vegetation type at Moor House, and is included under the general term mixed moor by Pearsall (1950). Calluna vulgaris was dominant on this level site, together with Eriophorum angustifolium, E.vaginatum, and Sphagnum spp.

4. Carecetum site (1800', 549m)

Adjacent to Trout Beck, this level site was dominated by Carex spp. and was typical of the marginal communities that separate calcareous flushes from the surrounding Blanket Bog. Little work on M.ater was carried out here as the site was too small an area to sustain further sampling after the three year study

by Hadley. However, as the site was in the shallow valley of Trout Beck, and sheltered by the valley sides to the south and the north, the temperature measurements were continued to determine the effect of this topography. These last two sites were used for comparative studies only.

5. Limestone Grassland Site (1825', 556m)

At the foot of Rough Sike, an outcrop of Tyne Bottom Limestone is overlaid by mineral soil, and supported a Festuca-Agrostis grassland containing Achillea millefolium, Carex caryophyllea, and Thymus drucei. This level site supported no population of M.ater but was used for the study of Tipula pagana Meigen.

6. Above Netherhearth (1850', 564m)

A site on the edge of the Blanket Bog with a slight slope of approximately 4^{o} to the west, and dominated by E.vaginatum and E.angustifolium, which formed dense tussocks in places. M.ater and T.subnodicornis did occur but this site was only used for temperature measurements.

The Dun Fell Sites

These sites were chosen to be as similar as possible with respect to aspect and vegetation, so that the climatic effects at the different altitudes could be more easily detected. They are all referred to by their altitude.

1. 1200' site (366m)

This was not on the nature reserve and was used for temperature measurements only. The site was adjacent

to the track leading from Knock village to the fell gate at the reserve boundary and was dominated by ungrazed Poa spp. and Holcus spp.

2. 1400' Site (427m)

A site dominated by J.squarrosus and inclined at approximately 3° to the west, well drained, and also supporting Festuca spp. and Vaccinium myrtillus. Sheep frequently collected here and the site underwent considerable trampling as a result, although no specific effect of this was detected.

3. 1700' Site (518m)

A level site dominated by J.squarrosus but much wetter than any other of the sites in this group. Drainage was impeded by rock at approximately 30 to 50cm below the surface and the site was surrounded by several stagnant pools. E.angustifolium was common here together with V.myrtillus, Empetrum nigrum, Potentilla erecta, Gallium saxatile, and Polytrichum commune.

4. 1900' Site (579m)

A well drained site, similar to 1400' but with no slope and a very uniform cover of J.squarrosus. V.myrtillus and Festuca spp. were also present but were not common. This site supported high densities of both M.ater and T.subnodicornis and was noted to have an abundant soil fauna in general.

5. 2050' Site (625m)

It was not possible to locate a convenient level area, dominated by J.squarrosus between 1900' and

Plate 1. The 1900' site is in the foreground and the valley of Knock Ore Gill in the background. To the right of the valley, the horizon is formed by the western slope of Knock Fell.

Plate 2. The 2050' site, showing its situation in the valley of Knock Ore Gill.

2500', and so a compromise site, which nonetheless supported a population of M.ater, was adopted. This site was inclined at about 5° to the north west and had an alluvial soil underlaid by gravel in places. The site was on the southern side of the Knock Ore Gill valley and the ground rose away steeply to the North and South. Deschampsia caespitosa and Holcus lanatus were dominant together with Gallium saxatile, Potentilla erecta, Rumex acetosella, Ranunculus acris, and Polytrichum commune.

6. 2500' Site (762m)

While the last five sites truly belonged to the scarp slope of Great Dun Fell, albeit on more or less level areas, and were to some extent sheltered from the east, this site was slightly over the summit ridge to the eastern side, and was situated due north of the summit of Knock Fell. J.squarrosus dominated this level area which showed a tendency towards waterlogging. Owing to access difficulties, detailed studies were discontinued here in 1969, although temperature measurements were maintained.

7. 2700' Site (823m)

A fairly well drained and level site, representing the highest altitude at which a large enough area dominated by J.squarrosus could be found. Eriophorum angustifolium and E.vaginatum were common, and were thought to be becoming more so during the study period. The site was sheltered to the north and the east by the summit of Great Dun Fell.

8. 2780' Site (847m)

Situated on the almost level summit of Great Dun Fell and about 100 yards from the nearest radio station building. Festuca spp. were dominant on a thin fell top podsol soil. This site was extremely exposed, with no shelter in any direction. It did not support a population of M.ater and was used only for temperature measurements.

3. TEMPERATURE MEASUREMENTS

3.1 Introduction

The original information on the climate over the Moor House National Nature Reserve came from the meteorological observations of Manley (1936, 1942, 1943) both at Moor House itself and on Great Dun Fell. He commented on the practical difficulties of making high altitude observations, some of which have been experienced in the present study. Manley measured air temperature in a standard Stevenson Screen at Moor House at 1840' O.D., and in 1936 produced the first precise set of data for a high altitude station in England.

He found mean temperatures differing by about 5.5°F (3.1°C) from lowland stations both at Appleby in the Vale of Eden and at Durham City. This mean difference was not, however, consistent over the whole temperature range, the mean maximum at Moor House being 7.0°F (3.9°C) lower and the mean minimum being 3.3°F (1.8°C) lower. On calm nights when cold air flowed down the South-East gradient into the Tees Valley from Moor House, a temperature inversion occurred giving higher minima at Moor House than at the lowland stations. Manley also commented on the "Holm Wind", a well known local phenomen which occurs on the western scarp slope of the Pennines as cold air from the summit ridge descends to the Vale of Eden.

The 1942 paper presented similar observations from a few feet below the 2780' summit of Great Dun Fell.

The mean daily temperature range in December was slightly less than 6°F (3.3°C) and in May and June it was 12°F (6.7°C). These values were approximately 66% of those obtained from well exposed lowland stations, e.g. Newton Rigg, 14 miles west of Great Dun Fell.

Manley (1943) presented further information on inversion and discussed katabatic air flow. Inversions occurred only on calm nights and numbered about 30 per year. More particularly relevant to the present study is the observation that the flow of cold polar air that produced the conditions of extreme cold on Great Dun Fell was not conducive to inversion formation.

Manley's observations were of course mainly concerned with air temperatures, and these and other observations have been continued at Moor House and Great Dun Fell. Daily observations from these two stations are published by the Meteorological Office and climatological averages have been published since 1951. By their very nature such meteorological observations are concerned with above ground measurements and the problem remains, in a study such as the present, of obtaining, and subsequently understanding, direct measurements of soil temperature. Macfadyen (1963) stressed this latter problem and pointed out that even where climatic factors in the vicinity of animals were measured there was not an exact correspondence between the readings obtained with instruments, and the influences which were significant for the animals.

An understanding of some of the temperature differences that can exist both within and between study sites is obtained by considering something of the relationship between air and ground conditions. Rider (1957) discussed the physics of soil temperature and stated that the soil surface derived most of its heat from the sun, the incident radiant energy depending upon a variety of factors including time of day, atmosphere, aspect, and the density and colour of the vegetation. He showed that the resulting temperature, which primarily concerns the biologist, is governed by a complex of factors, including the heat capacity of the soil and the heat dissipation within the soil. Interestingly, the specific heat of dry soil varies little with type, e.g. sand or peat, but thermal capacity does increase with an increase in water content and the maximum amount of water that a soil can hold can vary very much between different soil types. Moorland soils are noted for their high water content, and the higher the thermal capacity for a given amount of incident radiant energy, the lower will be the temperature.

The Present Study

The climate of the reserve is typical of the montane regions of Britain (Pearsall 1956), and has been described by Manley (1936) as sub-arctic, having many features comparable to those at sea-level in southern Iceland.

Clearly, soil temperature is of prime importance in controlling egg, larval, and pupal development of crane-flies, while air temperature will affect adult activity during the emergence period. Only in conditions of summer drought when the surface peat of the moor becomes dry does precipitation have a direct effect on the animals, although it does have an effect on soil temperature. Other climatic factors such as wind and sunshine only have a secondary effect through their influence on soil temperature. In this study most effort has been directed to the measurement of soil temperature.

3.2 The Cambridge Thermographs

During 1967 and the earlier part of 1968 two standard Cambridge mercury in steel thermographs were available and from September 1968 a further two instruments were loaned by the Nature Conservancy. In all cases the tubular thermometer bulbs, each approximately 1.5cm in diameter, were positioned immediately below the soil surface. This latter is difficult to ascertain in the field and in the present study the main criterion was that the bulbs should not be exposed to incident solar radiation and this resulted in the upper surface of the horizontal probe being some 0.5cm below the surface, and the probe as a whole being at a mean depth of about 1cm. Each circular chart contained one week's data but it

was found that the clockwork mechanism that turned the chart would run for more than two weeks and so sometimes the chart was allowed to turn through two revolutions.

In 1967 the thermographs were placed in extreme situations, one at the Peaty Gley site (1800') and the other at the 2700' site on Great Dun Fell. Measurements were only obtained during June and July, that is, during the adult emergence period.

In 1968 a fairly complete set of measurements from June to December were obtained from 1700' on Great Dun Fell, and also from 1900' and 2050' during the period September to December. Unfortunately the thermograph sited at 2700' failed and no measurements were obtained from it.

The 1969 data are more complete with continuous measurements from April to August at 1700', 1900', and 2050' and from May to August at 2700'. The recorders were frequently callibrated using a mercury in glass thermometer placed adjacent to the thermograph bulb.

3.2.1 Results

Maximum and minimum temperatures for each day have been extracted from the thermograph charts, the values being read to the nearest whole degree. These daily temperatures will be used in the later section concerned with adult emergence, but for the present purpose of comparing the climates at the different study sites they are presented in Tables 1, 2, 3 as weekly means, i.e.

$\frac{1}{2}$(max + min), together with, for 1967 only, the weekly average of the maxima and minima. The weekly mean values are illustrated in Figures 1, 2, and 3,

TABLE 1. 1967 Thermograph Results - Weekly Averages (°C) of Soil Temperature at 1cm depth

	Peaty Gley			2700'		
Dates	Max.	Min.	Mean	Max.	Min.	Mean
29. 5- 4.6	11.5	7.6	9.6	12.0	7.0	9.5
5. 6-11.6	12.0	6.9	9.5	10.3	5.8	8.1
12. 6-18.6	17.0	9.0	13.0	18.9	10.0	14.5
19. 6-25.6	14.3	9.7	12.0	11.6	8.7	10.2
26. 6- 2.7	13.9	9.9	11.9	10.9	7.9	9.4
3.7 - 9.7	13.7	10.0	11.9	11.3	9.2	10.3
10.7-16.7	14.5	11.1	12.8	13.8	9.4	11.6
17. 7-23.7	13.5	11.4	12.5	14.0	9.6	11.8
24. 7-30.7	14.2	11.3	12.8	11.3	9.7	10.5

TABLE 2. 1968 Thermograph Results - Weekly Means (°C) of Soil Temperature at 1cm depth

Dates	1700'	1900'	2050'
22. 9-28. 9		10.4	9.9
29. 9- 5.10		10.4	9.5
6.10-12.10	9.7	9.5	8.6
13.10-19.10	6.6	6.4	7.1
20.10-26.10	9.8	8.7	8.5
27.10- 2.11	8.9	7.0	8.4
3.11- 9.11	1.7	1.3	3.4
10.11-16.11	2.6	1.9	3.6
17.11-23.11	3.4	2.7	3.9
24.11-30.11	5.1	3.6	4.8
1.12- 7.12	4.1	2.9	3.9
8.12-14.12	1.2	0.3	2.3
15.12-21.12	0.0	0.0	1.3

TABLE 3. 1969 Thermograph Results - Weekly Means (°C)

of Soil Temperature at 1cm depth

Dates	1700'	1900'	2050'	2700'
20. 4-26. 4	4.2	4.1	4.8	3.4
27. 4- 3. 5	4.9	4.8	5.8	4.2
4. 5-10.5	6.1	6.5	6.0	5.0
11. 5-17.5	8.7	8.5	8.7	6.5
18. 5-24. 5	6.9	6.6	7.1	6.5
25. 5-31.5	7.5	9.0	9.5	7.0
1. 6- 7.6	13.1	11.8	12.5	12.2
8. 6-14.6	10.4	10.7	11.4	10.1
15. 6-21.6	10.9	11.2	11.6	10.3
22. 6-28.6	10.6	11.2	11.1	9.9
29. 6- 5.7	11.4	11.4	10.8	9.9
6. 7-12.7	11.7	11.3	10.6	9.7
13. 7-19.7	13.5	13.5	12.1	13.0
20. 7-26.7	13.6	13.5	12.7	12.0
27. 7- 2.8	12.7	12.8	12.9	11.1
3. 8- 9.8	14.8	14.7	13.4	14.2
10. 8-16.8	15.1	14.9	14.0	14.4

The 1967 results comparing the Peaty Gley and 2700' sites show that for most of the time the latter is about 1.7°C colder than the former. It is interesting to note, however, that on one occasion, 11 to 18 June, the 2700' temperature at 14.5°C was some 1.5°C above the Peaty Gley mean. Similar effects like this have been recorded to a lesser extent in 1969 also, notably over the

Figure 1. The weekly mean soil temperatures, in ^{o}C, obtained from the thermographs operated at the Peaty Gley site and the 2700' site in June and July 1967.

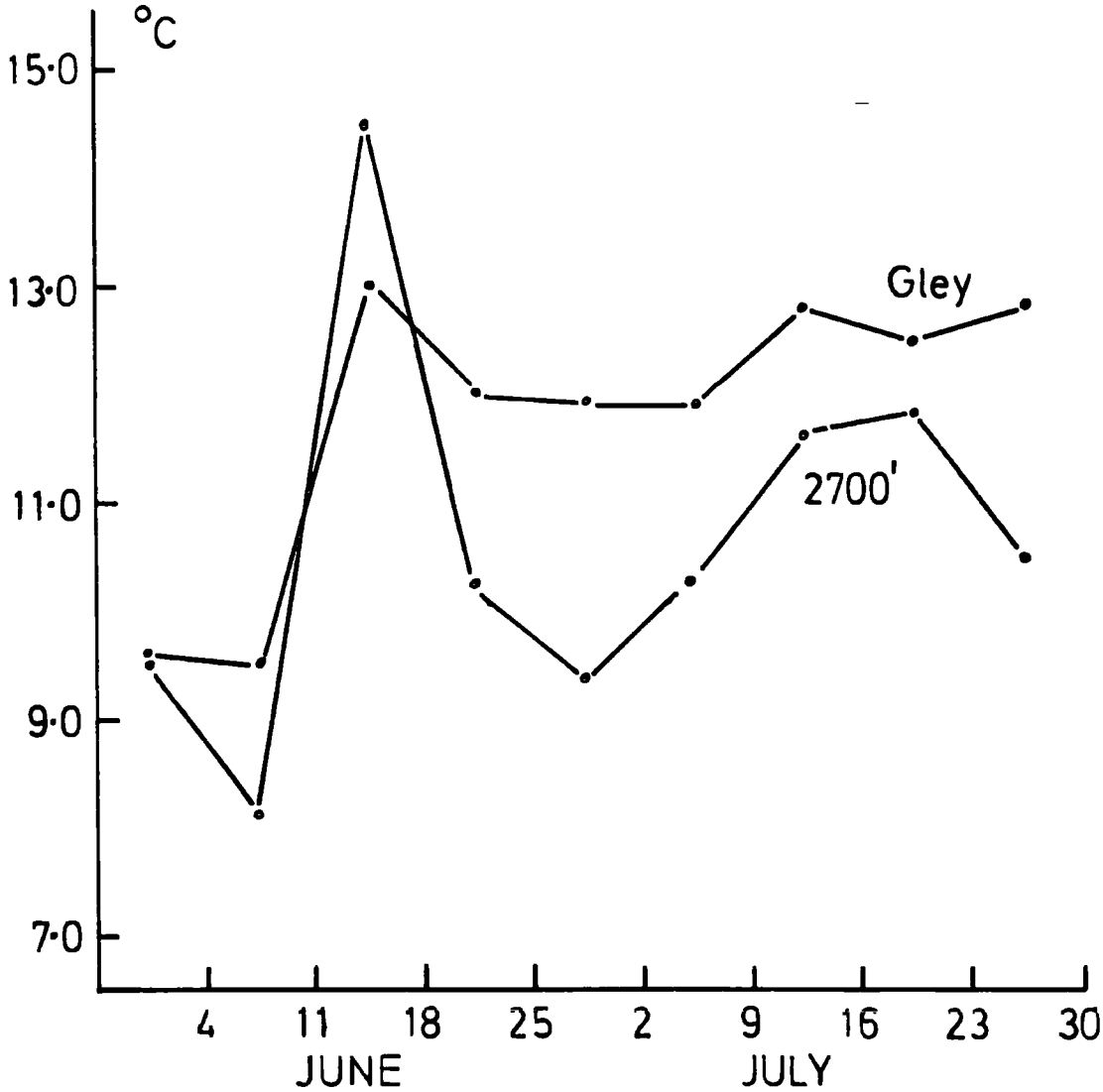

°C
15·0
13·0
11·0
9·0
7·0
Gley
2700'
4
11
18
25
2
9
16
23
30
JUNE
JULY

Figure 2. The weekly mean soil temperatures, in ^{o}C, obtained from the thermographs operated at the 1700', 1900' and 2050' sites in October, November and December 1968.

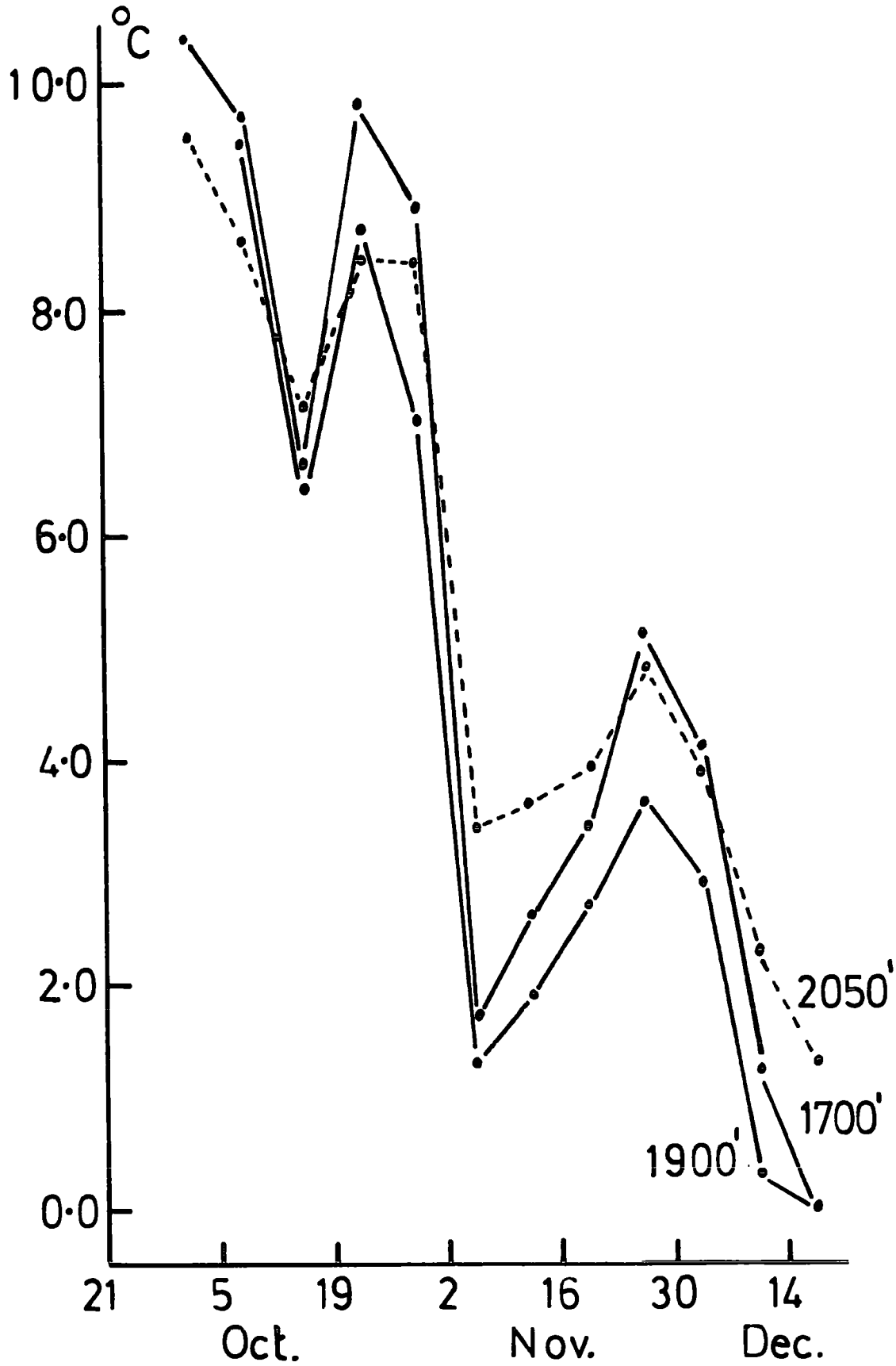

°C
10·0
8·0
6·0
4·0
2·0
0·0
2050'
1700'
1900'
21
5
19
2
16
30
14
Oct.
Nov.
Dec.

Figure 3. The weekly mean soil temperatures, in ^{o}C, obtained from the thermographs operated at the 1900', 2050', and 2700' sites in 1969.


15·0
°C
13·0
11·0
9·0
7·0
5·0
3·0
1900'
2700'
2050'
19
3
17
31
14
28
12
26
9
May
June
July
Aug.

period 31 May to 7 June when the 2700' temperature at 12.2°C exceeded the 1900' mean temperature and during 12 to 19 July and 2 to 9 August when it exceeded the 2050' means by 0.9°C and 0.8°C respectively. The precise reasons for this are not clear but it seems unlikely that inversion was responsible since, while during 11-18 June 1967 the mean minimum at 2700' was 1.0°C higher than at the Peaty Gley site, the mean maximum was 1.9°C higher. The lower temperature at the Gley site on this occasion could be due to higher water content and wind speed here.

The 1968 results for 1700', 1900', and 2050' show the 1900' temperatures to be an average of 1.0°C lower than the 1700' ones. The 2050' values are interesting in showing less extensive fluctuations than the other two sites. This results in the mean temperature at 2050' being higher than that at 1700' and 1900' after a fall in temperature from the previous weeks, and being lower than the other two sites after any corresponding rise. The different nature of this 2050' site has been discussed in Section 2, both in relation to aspect, soil and vegetation, and will be referred to again later in this section.

The most complete results were obtained from the thermographs in 1969, covering the period April to August. The weekly means obtained from 2700' were consistently lower than those from any of the other sites with the exception of the instances already noted. The 1900' temperatures are about 0.2°C lower than those at 1700' during the early and late parts of the record, but during

most of June they are above, by on average, a similar amount. This is in contrast to the 1968 findings where 1900' was some 1.0°C lower. In the absence of a complete year's thermograph records it is not possible at this stage to know whether this could be a genuine seasonal effect brought about by some change in the prevailing macroclimate or the vegetation, the 1968 data being collected during the last three months of the year while the 1969 results were from April to August. This topic will be considered further, later in this section.

Further indication of the interesting characteristics of the 2050' site is shown in the 1969 record. Generally the responses reported earlier occurred again, particularly over the period 17 to 24 May and 7 to 14 June where, after a fall in the mean temperature, 2050' became the warmest site. Conversely during 31 May to 7 June and 12 to 19 July, 2050' was colder than 1700' after a rise in temperatures generally.

One value of these thermograph records is that they give some indication of daily and weekly temperature fluctuations and allow some comparison of the accuracy of the second method of temperature measurement that is described below.

3.3 Chemical Temperature Integration

This method uses the inversion of a sucrose solution to a mixture of fructose and glucose, the rate of which is dependent on pH and temperature. Thus if the pH

is constant and the amount of inversion is known, an integration of the temperatures that the solution has experienced can be calculated. The method has been comprehensively reviewed by Lee (1969) and the version used in the present study is that due to Berthet (1960) with a modification described by Lawton (1969).

The velocity of the inversion is given by :

$$\log K = C_1 - \frac{C_2}{T} \qquad \text{-----(1)}$$

where : K = the velocity coefficient

C_1 = constant depending on the pH of the solution

C_2 = constant independent of pH

T = absolute temperature

Thus given the two constants it is only necessary to determine K for a value of T to be obtained. Pallman et al (1940) showed that for a sucrose solution :

$$K = \frac{1}{t} \log\left[\frac{A}{(A-X)}\right] \qquad \text{-----(2)}$$

where : t = time in days

A = initial concentration of sucrose

X = amount that inverts to glucose and fructose in time t

The concentration values can be determined polarimetrically and rotation angles substituted in (2) :

$$K = \frac{1}{t} \log\left[\frac{a_o - b_o}{a - b_o}\right] \qquad \text{-----(3)}$$

where : a_o = rotation angle at time = 0

a = rotation angle after time = t

b_o = rotation angle at complete inversion

Berthet discussed the difficulty of determining b_o and calculated a value of -9.10° which has been used in the present study. He also discussed the derivation of C_2 and showed that it could be taken as 5854 for the solution he specified. Lawton described how by transposing (1) :

$$C_1 = \frac{C_2}{T} + \log K$$

and if the value of K is found from solutions kept at constant temperatures, then T is also known, and since $C_1 = 5854$, then C_2 can be found. This removes the necessity of producing successive solutions of exactly the same pH and allows the pH to be changed a little without additional recalculation of the constants. A sucrose solution of pH 1.2 permitted exposure in the present study for about 30 days in the winter and 15 days in the summer. Where a longer interval was necessary in the summer, the pH was increased. There is considerable latitude in these values as they are designed to produce only half the maximum rotation of around 60°.

3.3.1 Practical Details

Two solutions were made up as specified by Berthet:

1. Buffer - 3.730g of KCl plus 33.9ml of N.HCl, the whole diluted to 500ml with distilled water
2. Sucrose - 400g of Analar sucrose dissolved in 260ml of distilled water plus 10ml of 35% formalin

The addition of the formalin was necessary to inhibit any bacterial action that would remove sucrose from the solution and also alter its pH. In the concentration used the formalin has little effect on the rate of inversion or the measured angle of rotation.

The two solutions were only mixed immediately prior to their use. Inversion is negligible in the primary sucrose solution, so a stock could be made up and stored for some time. After mixing the inversion solution was filtered. With experience it was found that 2" x 1" specimen tubes with polythene stoppers, placed inside fractionally larger aluminium specimen tubes with screw caps, were a satisfactory way of containing the solution in the field. The use of glass containers only was discontinued after repeated breakages, whether by the public or sheep. The solutions cannot be placed directly inside the aluminium tubes as reactions between the buffer and the metal occur.

Approximately 15ml of inversion solution was placed inside each tube and the tubes were then frozen at around $-25^{\circ}C$, in which state inversion is negligible. The tubes were transported to the field in vacuum flasks containing a freezing mixture and tubes removed from the field were similarly transported. In the field the tubes were positioned in the same manner as has been described for the thermograph probes. This method allowed measurement to be made at many sites in addition to those where the thermographs were maintained, but at these latter

sites the sugar tubes were positioned close to the thermograph probes to make comparison valid.

On Great Dun Fell, sucrose tubes were placed at the eight altitude sites described in Section 2. It was felt to be of interest that as wide an altitude range as was practical should be studied, as the literature of such studies is very restricted. On the Eastern side of the summit ridge tubes were maintained at all the Moor House sites that have been described in Section 2. A further tube was placed inside the Moor House Stevenson Screen for comparison with the temperatures recorded there.

One or two tubes were used to determine the a_o value, and one tube was placed in each of three constant temperature rooms at 5°C, 10°C, and 15°C to permit the calculation of C_1 mentioned previously. Angles of rotation were measured on a Bellingham and Stanley polarimeter. It is important to allow the sucrose solutions to warm up to room temperature after they have been unfrozen, prior to measurement, as the angle of rotation varies with temperature. Ideally the polarimetry should be carried out under constant temperature conditions but in the present study the near constant temperature of the polarimetry laboratory was found to be satisfactory.

3.3.2 Results

1. Accuracy

In constant temperature baths, Berthet (1960) found that temperatures obtained by the inversion did not vary by more than 0.3°C from those obtained by more

convential means. Lee (1969), in investigating the different factors that could lead to error, concluded that, overall, the probable precision of the method was $\pm$ 0.1°C. In the present study replicates were placed at some of the sites and their results are presented in Table 4.

TABLE 4. The Mean Temperatures obtained from Sucrose Tube Replicates

Period	Site	Mean Temperatures °C			
2.11 - 26.11.67	L. Grassland	2.6	2.3	2.6	
6. 4 - 24. 4.68	Peaty Gley	6.2	6.1	6.0	6.5
9.10 - 20.11.68	Bl. Bog	6.5	6.5	6.8	7.0

These replicates are considered satisfactory, though precisely how much of the variation at each site is due to microclimate differences must remain conjecture.

The main source of inaccuracy of this method is the exponential relationship between the rate of sucrose inversion and the temperature of the solution. This results in an overestimation of the arithmetic mean temperature on each occasion. The temperature value, T_e, obtained directly by the sucrose method has been variously referred to as the exponential, effective, or ecological mean temperature. Berthet suggested that, since the temperature coefficient of sucrose inversion is of the same order of magnitude as the coefficients for many biological reactions, the value T_e may be more

significant in many ecological studies than the arithmetic mean T_a. That this may be true is not disputed, but as Lee (1969) pointed out, such coefficients are valid only over restricted temperature ranges and it is difficult to relate the results obtained to other arithmetic measurements. Summarising the comparisons made between the true arithmetic temperature T_a, and the sucrose estimated temperature T_e, Lee showed that the range of temperature experienced by the solution was most important and that where this was less than $5^{\circ}C$ the values of T_a and T_e were virtually the same. In the present study it has been shown that while within any one month the soil temperatures are fairly constant, nonetheless there are occasions when a range in excess of $7^{\circ}C$ has been recorded. Further, the temperature range in the Moor House Screen was frequently much greater than this.

2. Estimating the arithmetic mean temperature

A simple linear regression has been performed of T_a on T_e so that for any value of T_e an estimate of T_a can be obtained. The measurements of T_a used in the regression come from situations where sucrose tubes were operated in conjunction with the Cambridge thermographs and with the thermometers in the screen. The values are given in Table 5 and illustrated in Figure 4. The equation of the line is :

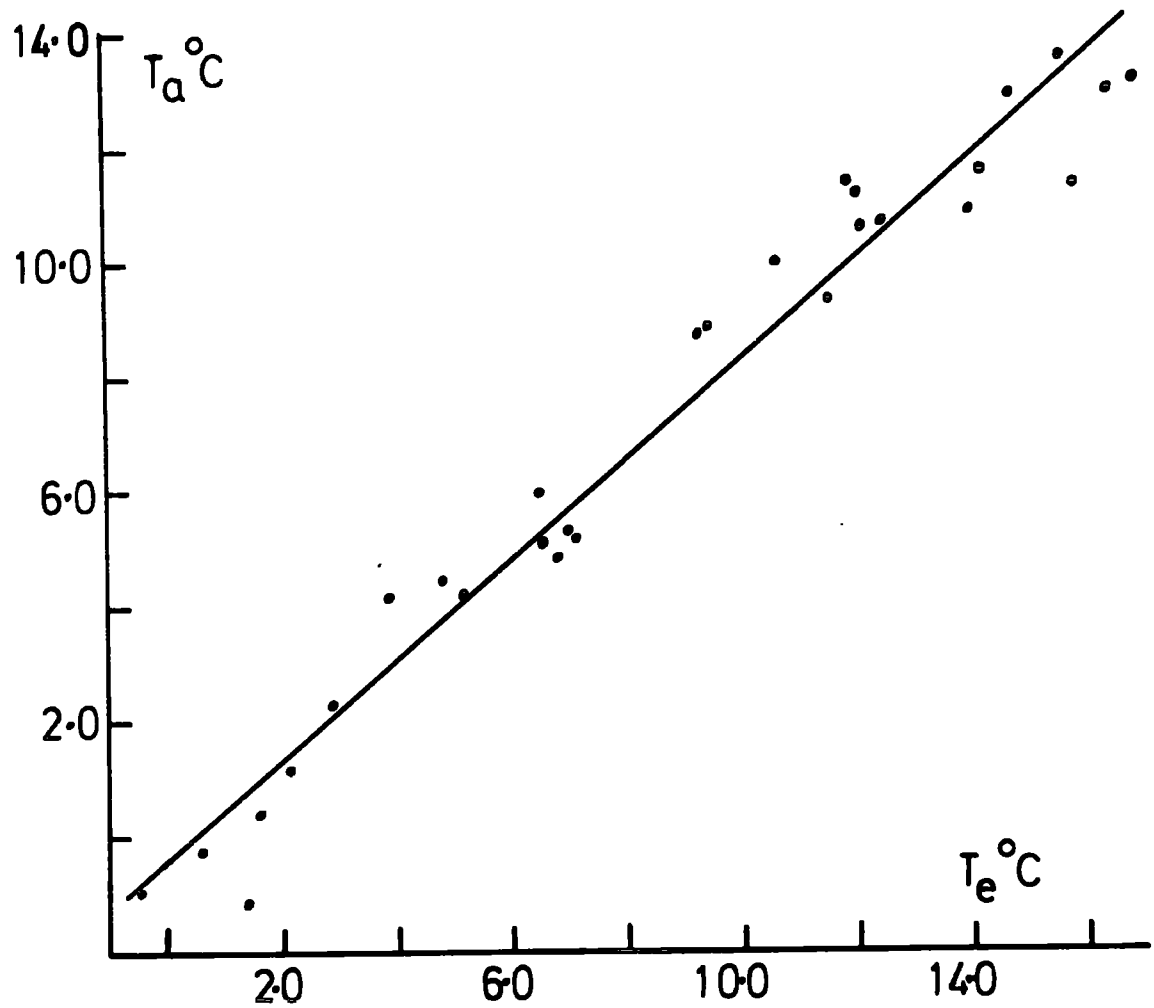
$$y = -0.4 + 0.87x$$

The correlation coefficient of $r = +0.98$ shows the close linear relationship between T_e and T_a (df. = 27, $P < 0.001$).

TABLE 5. The Relationship between the true arithmetic mean temperature, T_a, and that obtained by the sucrose method, T_e

Duration	T_e °C	T_a °C	Source of T_a
10.10 - 2.11.67	4.8	4.5	Met. Screen
2.11 -26.11.67	2.9	2.3	"
2. 1 -12. 3.68	-0.5	-0.9	"
12. 3 - 6. 4.68	2.1	1.2	"
6.4 -25. 4.68	5.2	4.2	"
25. 4 -23. 5.68	3.9	4.2	"
2. 7 -25. 7.68	10.6	10.0	"
25. 7 - 1. 9.68	12.1	10.6	"
1. 9.- 9.10.68	11.5	9.4	"
9.10 -20.11.68	6.5	5.2	"
20.11 -13. 1.68/69	1.6	0.4	"
13. 1 -13. 4.69	1.4	-1.1	"
13. 4 - 9.6. 60	7.0	5.3	"
9. 6 -16. 7.69	14.0	10.9	"
16. 7 -10. 8.69	16.4	13.0	"
10. 8 - 9. 9.69	15.8	11.4	"
9. 9 - 7.10.69	9.3	8.8	"
7.10 - 4.11.69	9.4	8.9	"
4.11 - 9.12.69	0.7	-0.2	"
2. 7 -25. 7.68	12.5	10.7	1700' Thermograph
"	12.0	11.2	2050' "
1. 9 - 9.10.68	11.9	11.4	2050' "
9.10 -20.11.68	7.1	5.2	1700' "
"	6.8	4.9	1900' "
"	6.5	6.0	2050' "
22. 7 - 5. 8.69	16.9	13.2	1700' "
"	15.6	13.6	1900' "
"	14.7	12.9	2050' "
"	14.2	11.6	2700' "

Figure 4. The regression of the true arithmetic mean temperature, T_a °C, on the mean temperature obtained by the sucrose method, T_e °C. The equation of the line is $y = -0.4 + 0.87x$ and the correlation coefficient, $r = +0.98$, is significantly different from zero, d.f. = 27, $P < 0.001$.


14·0
T_a °C
10·0
6·0
2·0
T_e °C
2·0
6·0
10·0
14·0

3. The Dun Fell Sites

The results obtained from the sucrose method have all been converted to the arithmetic mean T_a using the regression equation. They are presented in this latter form in Table 6 for the Dun Fell sites and in Table 9 for the Moor House sites.

TABLE 6. Arithmetic Mean Soil Temperatures (°C) from Sucrose Inversion. Each value represents the Mean Temperature from the Preceding Date

Dates	1200'	1400'	1700'	1900'	2050'	2500'	2700'	2780'	Mean
1.10.67									
30.10.67			5.9	5.7	5.5	4.3	4.1		
26.11.67			1.6	1.4	1.3	0.2	-0.1		
14. 1.68			-1.4	-1.4	-1.8	-2.2	-2.4		
31. 3.68			1.0	0.6	0.3	0.0	-0.3		
25. 4.68	5.0	4.4	4.4	3.3	3.5	3.3	2.6	1.3	3.6
23. 5.68	5.3	4.7	4.3	3.4	3.8	4.1	2.9	2.0	3.8
2. 7.68	9.1	8.9	8.3	8.1	8.3	8.0	7.5	7.3	8.2
25. 7.68	12.6	11.7	10.5	10.2	10.0	10.0	8.9	8.5	10.3
1. 9.68	10.5	10.3	10.1	10.0	10.0	9.9	8.6	8.3	9.7
9.10.68	11.1	10.9	10.3	9.9	10.0	9.5	8.6	7.0	9.7
20.11.68	6.6	6.3	5.8	5.5	5.3	4.7	4.5	4.3	5.4
13. 1.69	2.5	2.5	2.8	1.6	1.5	1.4)	0.4	-0.5	1.2
21. 4.69	1.9	2.1	1.1	0.6	1.3	0.8)			
9. 6.69	7.1	6.9	6.6	6.5	6.6	6.1	5.7	5.5	6.4
22. 7.69	12.6	12.2	12.0	11.7	11.9	12.1	10.9	10.7	11.8
5. 8.69	16.3	14.3	14.3	13.2	12.4	13.7	12.0	11.3	13.4
16. 9.69	14.8	14.7	14.5	14.4	14.7	14.5	14.1	12.4	14.3
14.10.69	10.7	9.2	8.9	9.1	8.1	8.1	7.3	7.1	8.6
2.12.69	4.6	5.3	4.7	4.5	4.5	3.3	2.8	2.5	4.0
27. 1.70	-0.8	-0.6	-1.1	-1.3	-1.1	-1.7	-1.7	-1.8	-1.3
19. 4.70	2.0	1.6	1.3	1.3	0.6	0.7	0.4	0.1	0.9
13. 5.70	7.4	6.7	6.4	5.7	5.7	5.3	4.7	3.2	5.6

Figure 5 illustrates the temperatures obtained from 1700' and 2700' over the period October 1967 to May 1970. Any attempt to represent all the Great Dun Fell data in this way produces confusion, but the graph does serve to show the annual temperature cycle. It is clear that the summer and winter extremes for 1969-70 were much higher and lower respectively than those for the 1968-69 period. The temperatures at the two illustrated sites follow each other fairly closely and always remain in the same order. The short term fluctuations shown by the thermograph record, when the 1700' temperature was exceeded by that at 2700', do not manifest themselves on this longer period record. Table 7 gives the maximum summer temperature and the minimum winter temperature for all the Great Dun Fell sites over the periods shown in 1968-69 and 1969-70.

TABLE 7. Maximum Summer and Minimum Winter Soil Temperatures °C.

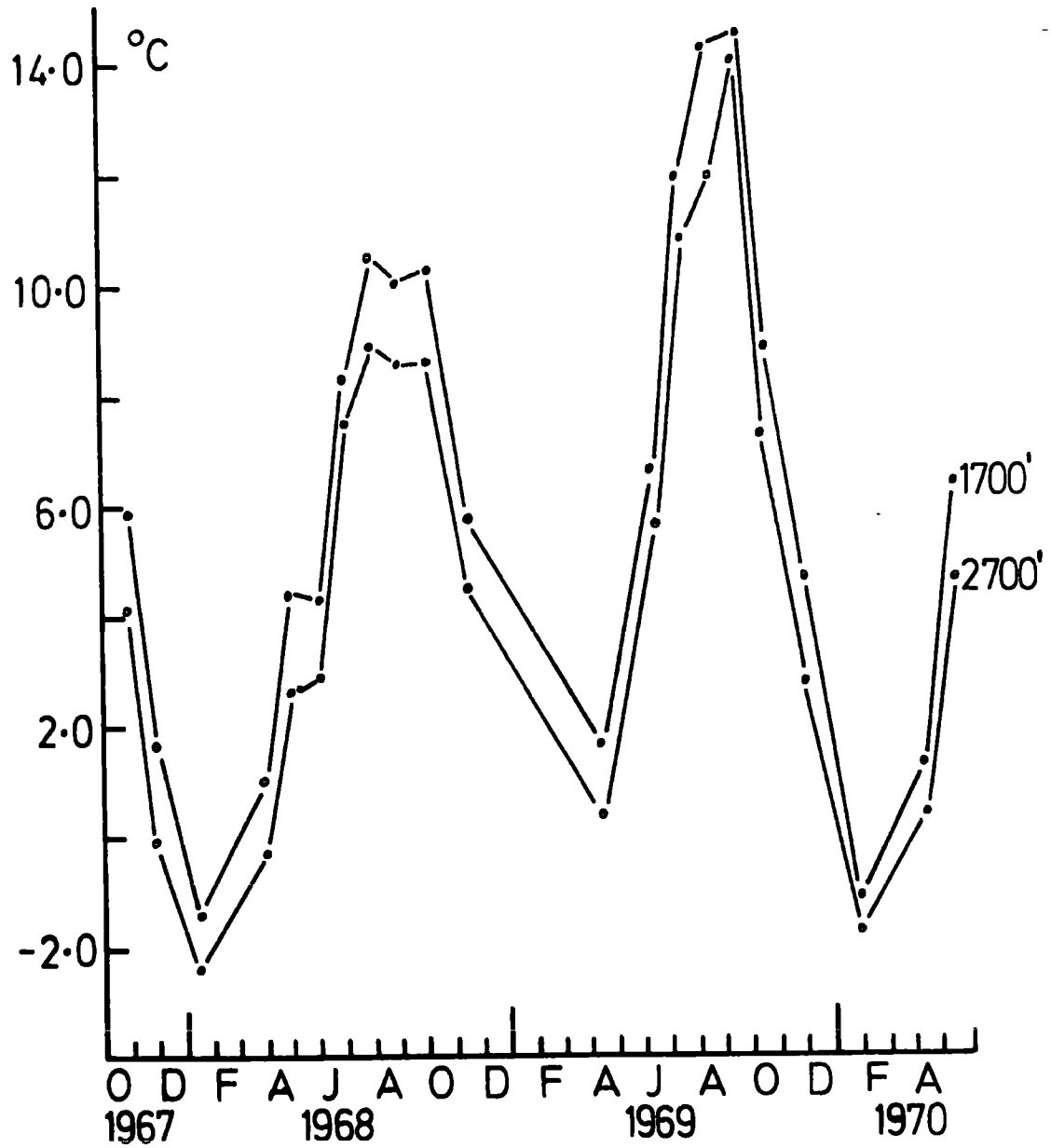
1968-69

Site	Max. 2-25.7.68	Min. 20.11-21.4.69	Range
1200'	12.6	2.1	10.7
1400'	11.7	2.2	9.5
1700'	10.5	1.7	8.8
1900'	10.2	1.0	9.2
2050'	10.0	1.4	8.6
2500'	10.0	1.0	9.0
2700'	8.9	0.4	8.5
2780'	8.5	-0.5	8.9

1969-70

	22.7-5.8.69	2.12-27.1.70	
1200'	16.3	-0.8	17.1
1400'	14.7	-0.6	15.3
1700'	14.5	-1.1	15.6
1900'	14.4	-1.3	15.7
2050'	14.7	-1.1	15.8
2500'	14.5	-1.7	16.2
2700'	14.1	-1.7	15.8
2780'	12.4	-1.8	14.2

Figure 5. The arithmetic mean soil temperatures, in ^{o}C, obtained by sucrose inversion at the 1700', and 2700' sites from October 1967 to May 1970.


°C
14·0
10·0
6·0
2·0
-2·0
1700'
2700'
O D F A J A O D F A J A O D F A
1967
1968
1969
1970

The consistent reduction of maximum and minimum temperature with increase in altitude is maintained over all the sites except 2050' where the minimum in 1968-69 and both the maximum and minimum in 1969-70 are not in the sequence. The maximum for 2500' in 1969-70 is also out of sequence. The thermograph temperatures obtained from 2050' have already been mentioned in this context and the results from both these sites will be discussed in greater detail later.

The range between the maximum and minimum at each site, while being higher overall in 1969-70, is fairly consistent for each period. There is some decrease of this range with increase in altitude; the 2780' range being 1.8°C less than the 1200' range in 1968-69 and 2.9°C lower in 1969-70. This could be due to the longer periods of cloud cover at the summit disproportionately lowering the summer temperatures and prolonged snow cover in the winter having an insulating effect. Geiger (1951) shows the modifying effect these two factors can have in producing a more equable climate.

In order to illustrate more clearly the differences between the altitude sites, the temperatures from five of them are shown in Figure 6, expressed as their variation from the mean of the eight temperatures recorded for each period. This mean temperature is given in the last column of Table 6. To simplify the presentation of the data and show what are thought to be valid differences, the results have been collected into groups of 0.3°C according to the scheme :

$-0.1 - +0.1 = 0.0$

$0.2 - 0.4 = 0.3$

$0.5 - 0.7 = 0.6$

$0.8 - 1.0 = 0.9$

$1.1 - 1.3 = 1.2$ etc.

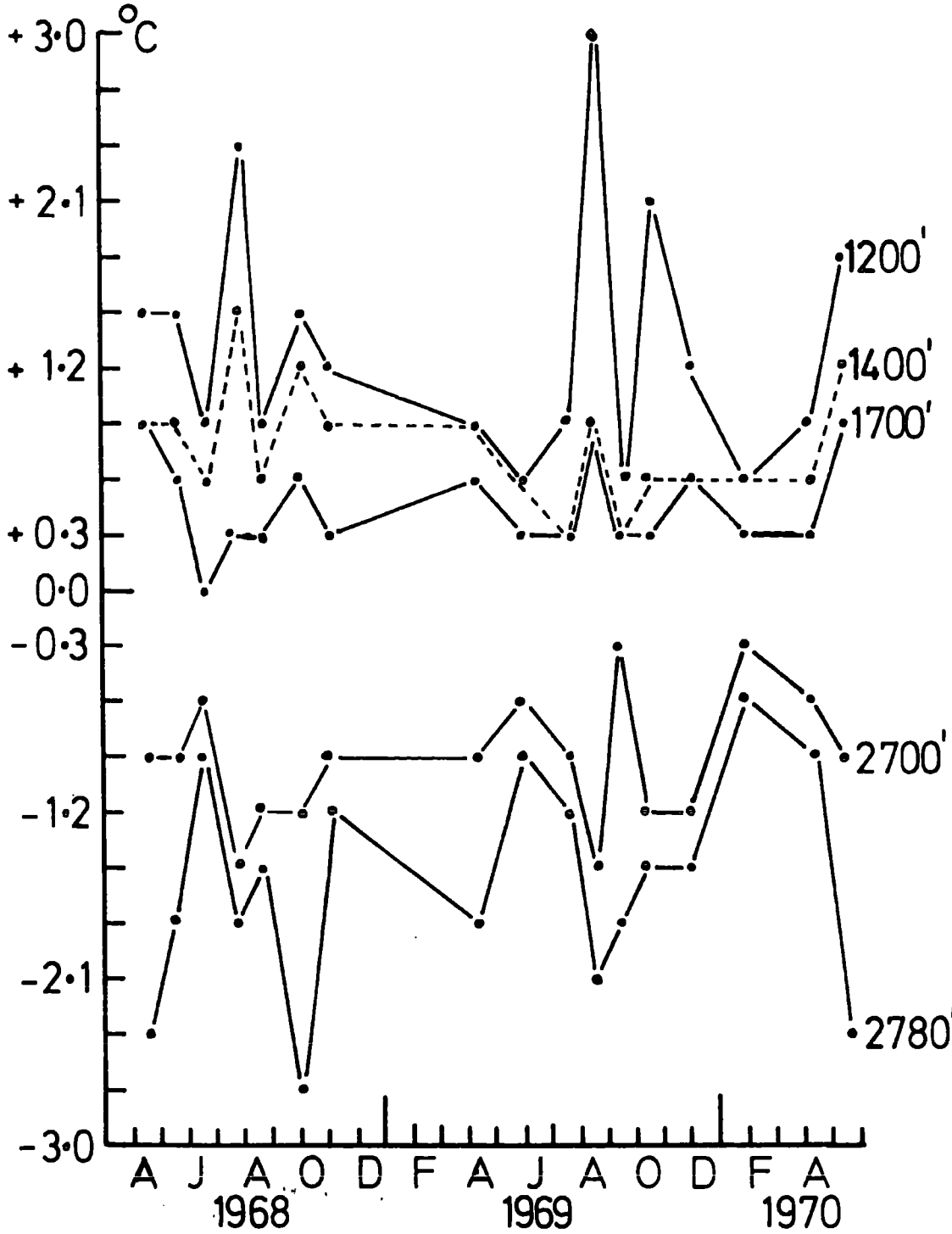
Clearly, if there were a constant difference in temperature with change in altitude on Great Dun Fell, a straight line for each site would be obtained. Figure 6 shows that this is obviously not so. The results from 2050', 1900', and 2500' are not included in this figure as they merely confuse what is already a complicated picture.

The following salient features emerge from the data presented for the eight Great Dun Fell study sites and considered according to the grouping scheme presented earlier :

1. For the six study sites other than those at 2050' and 2500' there is a decrease in temperature with increase in altitude, except on a few occasions when the divergence from this pattern is never greater than 0.3°C. The results from 2500' are up to 0.6°C colder than the mean during the period August to April 1968-69 and 1969-70. During the remaining parts of the study, however, the 2500' temperatures are sometimes up to 0.3°C above the mean. The 2050' temperatures to some extent behave in an opposite manner and tend to be warmer than the mean during the August to April periods and colder at the other times.

2. As has been remarked earlier, this general decrease of temperature with increase in altitude is of different magnitudes over different periods. Thus, during the period

Figure 6. The mean soil temperatures, in ^{o}C, at the 1200', 1400', 1700', 2700', and 2780' sites, expressed as their variation over each sucrose inversion period, from the mean temperature of the eight Dun Fell sites. The data have been collected into units of $0.3^{o}C$ according to the scheme described in the text.


°C
+ 3·0
+ 2·1
+ 1·2
+ 0·3
0·0
- 0·3
- 1·2
- 2·1
- 3·0
1200'
1400'
1700'
2700'
2780'
A J A O D F A J A O D F A
1968
1969
1970

December 1969 to January 1970 all the temperatures were within $\pm 0.6^{\circ}C$ of the mean so that the difference between 1200' and 2780' was only $1.2^{\circ}C$. During May 1969 the same situation occurred again, with the exception of 2780' which was $0.9^{\circ}C$ below the mean. The period August to September 1969 showed a similar convergence to the mean, to establish the smallest difference in temperature between 1200' and 2700' recorded during the study, namely $0.9^{\circ}C$. Conversely, there appear to be definite periods when the temperatures diverge from the mean and the greatest ranges between the highest and the lowest sites occur. This divergence is particularly noticeable during July 1968 with the 1200' temperature $2.4^{\circ}C$ above the mean and the 2780' temperature $1.8^{\circ}C$ below it, giving a range of $4.2^{\circ}C$. This range was exceeded during the last week in July and the first week in August 1969 when 1200' was $3.0^{\circ}C$ above the mean and 2780' $2.1^{\circ}C$ below it, producing a range of $5.1^{\circ}C$.

3. It has already been stated that the summer and winter of 1969-70 were both more extreme than during 1968-69. To permit some comparison between the intermediate seasons, Table 8 gives the mean temperatures recorded over approximately three month periods corresponding roughly to the seasons of the year. It is acknowledged that the periods are not strictly comparable, but the timing of the inversion dates was largely determined secondarily by visits in the course of the biological study.

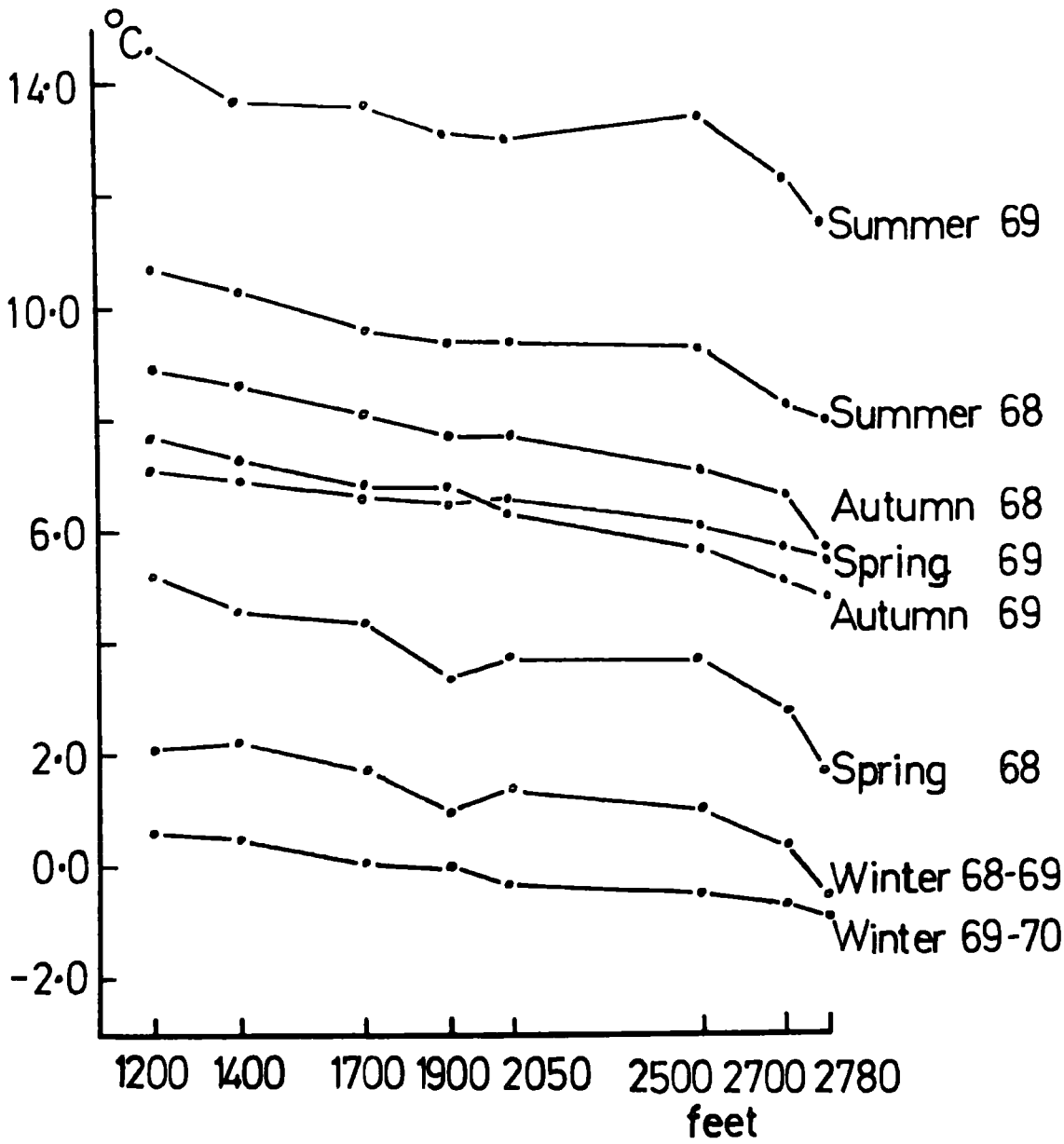
TABLE 8. Seasonal Mean Soil Temperatures on Great Dun Fell, °C.

Season	1200'	1400'	1700'	1900'	2050'	2500'	2700'	2780'
Spring 68	5.2	4.6	4.4	3.4	3.7	3.7	2.8	1.7
Summer 68	10.7	10.3	9.6	9.4	9.4	9.3	8.3	8.0
Autumn 68	8.9	8.6	8.1	7.7	7.7	7.1	6.6	5.7
Winter 68/69	2.1	2.2	1.7	1.0	1.4	1.0	0.4	-0.5
Spring 69	7.1	6.9	6.6	6.5	6.6	6.1	5.7	5.5
Summer 69	14.6	13.7	13.6	13.1	13.0	13.4	12.3	11.5
Autumn 69	7.7	7.3	6.8	6.8	6.3	5.7	5.1	4.8
Winter 69/70	0.6	0.5	0.1	0.0	-0.3	-0.5	-0.7	-0.9

These temperatures are illustrated in Figure 7 which shows that while Summer 1969 was about 3.5°C warmer than Summer 1968, Winter 1969-70 was only about 2.0°C colder than Winter 1968-69. Spring 1968 appears to be cold in relation to the other seasons but the other remaining three seasons, namely, Autumn 1968 and 1969 and Spring 1969 are of a similar temperature. Once again the aberrant behaviour of the 2050' and 2500' sites is illustrated, producing, on this seasonal basis, relatively higher temperatures on several occasions. On two of these, however, Spring 1968 and Winter 1968-69, this is accentuated by the sharp drop in temperature between 1700' and 1900'.

When it is remembered that the majority of the sites were chosen to be as similar as possible at the different altitude stations, the temperature results are perhaps what would be expected. The 1700', 1900', and 2700' sites are level areas, on the western side of Great Dun Fell, dominated

Figure 7. The seasonal mean soil temperatures, in ^{o}C, at the eight Dun Fell sites, from summer 1968 to winter 1969-70.

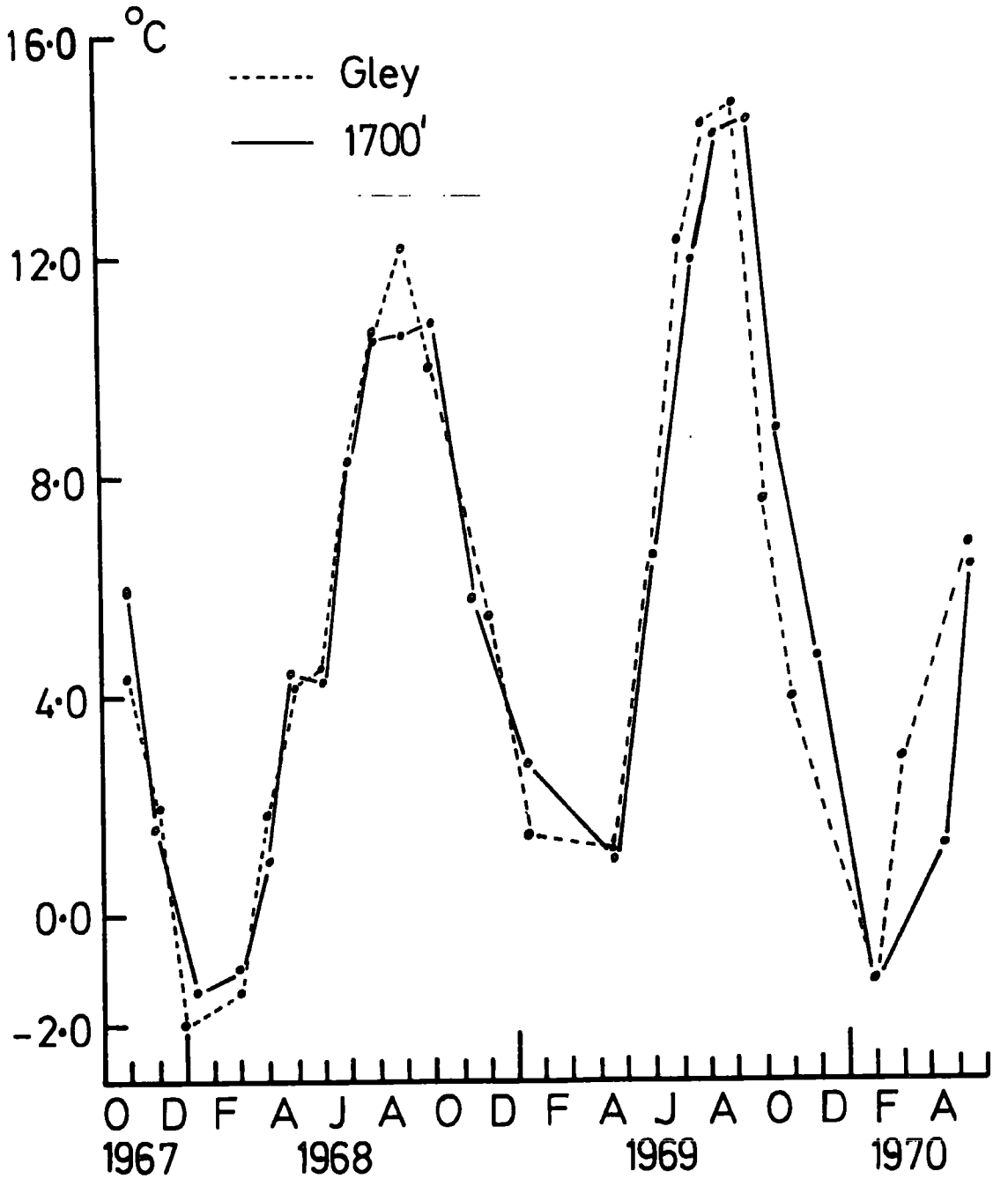

°C.
14·0
10·0
6·0
2·0
0·0
-2·0
Summer 69
Summer 68
Autumn 68
Spring 69
Autumn 69
Spring 68
Winter 68-69
Winter 69-70
1200 1400 1700 1900 2050 2500 2700 2780
feet

by Juncus squarrosus. The 1200' site is situated off the reserve, under longer meadow grass, by the road leading to the reserve gate. The 2050' site is clearly different. Its north-westerly slope on the side of Knock Ore Gill will produce greater afternoon warming from direct sunlight, while the clay soil and different vegetation are other factors which have been noted earlier to affect the heat relationships of any area. The 2500' site, again, does not really belong to the general series, for while it is level and J.squarrosus is dominant, it is not on the western side of the reserve, being over the summit ridge and sheltered from the west and south by Knock Fell. 2780', where the temperature is frequently much colder than at 2700', is under short Festuca grassland at the summit of the fell. Unlike any of the other sites it is thus equally exposed to winds from all directions whose additional cooling effect may account for the coldness of this site.

4. Moor House Mean Temperatures from Sucrose Inversion

The arithmetic temperatures for the six study areas in the vicinity of the house are presented in Table 9, together with the mean of these sites for each inversion period. There is naturally much less variation between these temperatures as the sites are all at approximately the same altitude; 1800'. It is differences in slope, aspect, and vegetation cover that are mainly responsible for any temperature variation between the sites. The temperatures from the Peaty Gley site are presented in Figure 8 for the period October 1967 to May 1970 and are compared with the temperatures obtained over the

Figure 8. The arithmetic mean soil temperatures, in ^{o}C, obtained by sucrose inversion at the Peaty Gley site and the 1700' site from October 1967 to May 1970.


16·0
°C
Gley
1700'
12·0
8·0
4·0
0·0
-2·0
O D F A J A O D F A J A O D F A
1967
1968
1969
1970

same period from the 1700' site on Great Dun Fell. Both sites are level and dominated by J.squarrosus. There is a close correspondence between the two sites, most of the differences in the figure being probably due to the slightly different measuring periods.

TABLE 9. Arithmetic Mean Soil Temperatures, °C, from Sucrose Inversion. Each value represents the mean temperature from the preceding date

Dates	P.Gley	B.Bog	A.Neth.	Podsol	Carem.	L.Grass	Mean
10.10.67							
2.11.67	4.3	4.3	4.6	4.7	4.6		
26.11.67	2.0	1.9	2.1	3.2	2.4	1.6	2.1
2. 1.68	-2.0	-2.1	-1.8	-1.4	-1.8	-2.1	-1.9
12. 3.68	-1.4	-1.4	-1.3	-1.1	-1.4	-1.4	-1.3
6. 4.68	1.8	1.6	1.3	1.7	2.0	1.4	1.6
25. 4.68	4.2	3.8	4.1	4.3	5.0	4.0	4.2
23. 5.68	4.5	4.0	4.0	4.6	5.4	4.5	4.5
2. 7.68	8.1	7.5	8.2	8.4	8.5	8.0	8.1
25. 7.68	10.6	9.6	9.8	10.6	10.9	10.7	10.4
1. 9.68	12.2	10.8	10.5	11.7	11.6	11.6	11.4
9.10.68	10.0	8.0	7.4	12.0	10.6	9.8	9.6
20.11.68	5.5	5.4	5.8	6.6	5.3	5.7	5.7
13. 1.69	1.5	1.6	1.4	1.9	1.5	1.3	1.6
13. 4.69	1.2	1.0	1.0	1.5	1.4	0.4	1.1
9. 6.69	6.6	6.4	6.4	6.8	6.9	6.7	6.6
16. 7.69	12.3	11.8	11.9	12.6	12.4	12.0	12.2
10. 8.69	14.5	14.5	14.2	14.5	14.4	14.3	14.4
9. 9.69	14.7	12.5	14.0	14.5	14.4	13.9	14.0
7.10.69	7.6	8.2	7.8	8.6	8.8	8.6	8.3
4.11.69	8.0	7.5	7.6	7.6	8.0	7.5	7.7
9.12.69	2.6	1.2	1.3	2.7	1.8	1.2	1.8
20. 1.70	-1.1	-0.5	-0.5	-0.7	-0.4	-0.7	-0.7
24. 2.70	2.9	3.5	1.4	2.3	3.1	0.4	2.3
18. 5.70	6.8	5.4	5.3	6.4	6.3	5.7	6.0

Table 9 shows that while between site differences are small, two sites, the Carecetum and Peaty Podsol, are fairly consistently warmer than the mean, while two others,

the Blanket Bog and Above Netherhearth sites, are mainly colder than the mean. The remaining two sites, the Limestone Grassland and Peaty Gley, follow the mean much more closely. The average variation from the mean over the study period is given in Table 10.

TABLE 10. Average Variation from the Mean Temperature of the Six Moor House Sites, 10.10.67 to 18.5.70.

Site	Average Variation °C
Peaty Podsol	+ 0.4
Carecetum	+ 0.3
Peaty Gley	+ 0.2
Limestone Grassland	- 0.2
Above Netherhearth	- 0.3
Blanket Bog	- 0.3

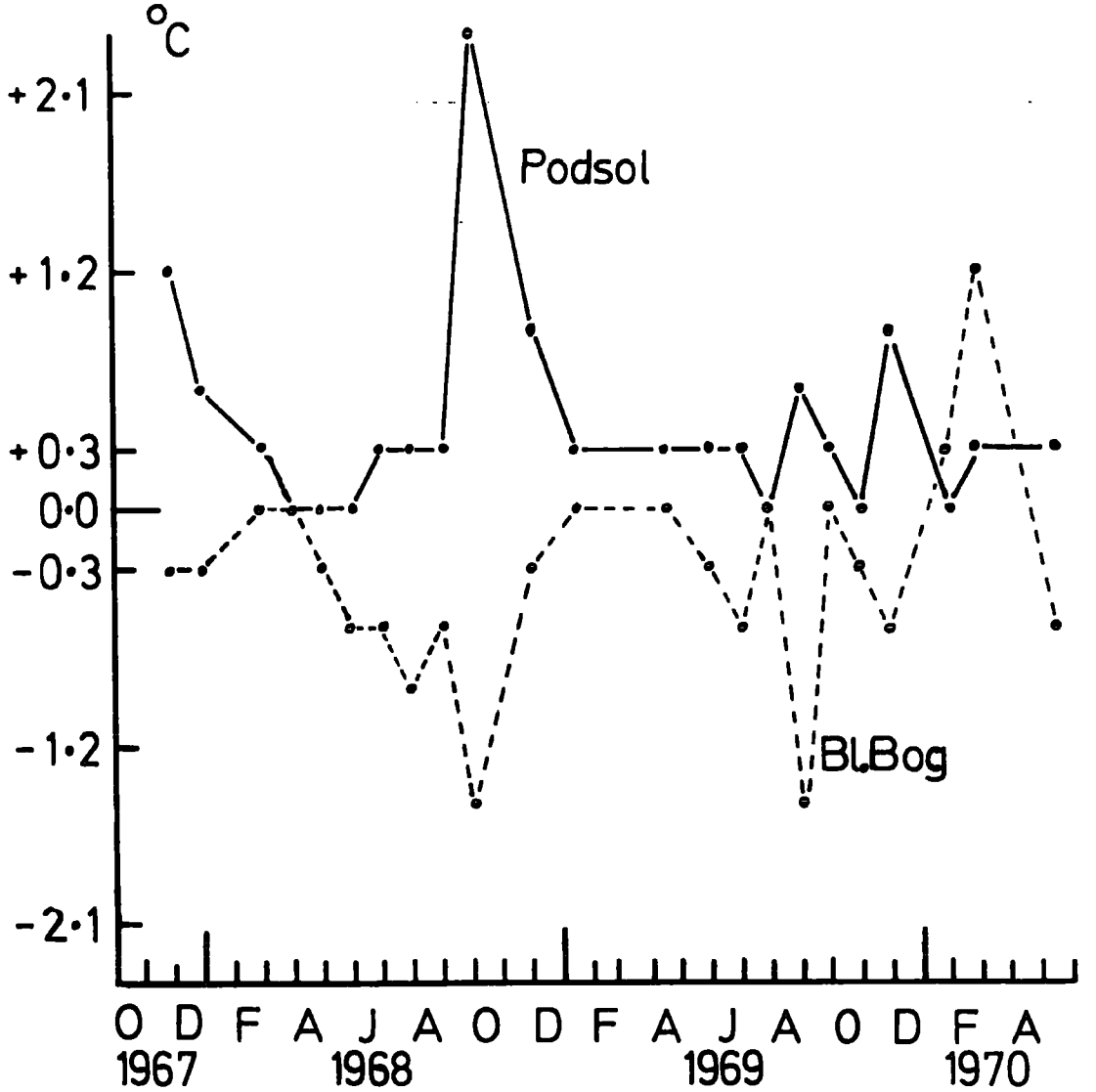
Thus, over the period October 1967 to May 1970 the maximum average difference was 0.7°C between the Peaty Podsol and Blanket Bog sites. Given the descriptions of the sites in Section 2, the results in Table 10 seem intuitively reasonable. The Podsol and Gley sites are both dominated by J.squarrosus but while the Gley is level, the Podsol is on a SSE slope of 7°. The Carecetum is in the sheltered valley of the Trout Beck. The relative coldness of the Blanket Bog site is perhaps best explained by its wetness with a higher degree of evaporative cooling from the Sphagnum surface, and the increased shading afforded by Calluna vulgaris and Eriophorum spp. which dominate this site. A similar shading effect, though this time only by Eriophorum could also account for the Above Netherhearth results.

The variation from the mean of the Peaty Podsol and Blanket Bog sites is illustrated in Figure 9, with the data grouped as described previously. Some effects similar to those occurring on Great Dun Fell are illustrated in this figure.

Although for most of the time the Podsol is warmer than the Bog, the difference between the two sites varies considerably. Thus, during the period January to March 1968 they were never more than 0.3°C above and below the mean respectively. A similar situation occurred between December 1968 and April 1969, while during December 1969 to March 1970 the Bog became warmer, at 1.2°C above the mean, than the Podsol which was only 0.3°C above the mean. Conversely, there are periods when the temperatures diverge from the mean; notably September to October 1968, when a 3.9°C temperature difference existed between the two sites, and August to September 1969 when a 2.1°C difference developed.

The 3.9°C value is particularly high and can be compared with the 4.2°C difference which developed at about the same time between the 1200' and 2780' sites on Great Dun Fell. It is interesting to note that the times of divergence from the mean occur at about the same time each year; summer and autumn, for both the Moor House and Great Dun Fell stations. Similarly, the times of convergence occur during winter and spring.

Figure 9. The mean soil temperatures, in ^{o}C, at the Peaty Podsol and Blanket Bog sites, expressed as their variation over each sucrose inversion period from the mean temperature of the six Moor House sites. The data have been collected into units of $0.3^{o}C$ according to the scheme described in the text.


°C
+2·1
+1·2
+0·3
0·0
-0·3
-1·2
-2·1
Podsol
Bl.Bog
O D F A J A O D F A J A O D F A
1967
1968
1969
1970

3.4 Discussion

The temperature data presented have been collected as part of an ecological study of crane-fly populations, which has naturally tended to limit the records to those which would be biologically useful. The incomplete data from the Cambridge thermographs are useful to show something of the weekly variation that can occur at different sites and particularly illustrate the behaviour of the 2050' site in both warming and cooling more slowly than the other sites so that superimposed on its mean is a reduced excursion of temperature between maximum and minimum. This presumably is a reflection of the site's thermal capacity while the mean temperature, like that of all the other sites, is produced by the interaction of exposure to sunshine and warm air together with the cooling effects of air movement, and radiation.

The sucrose tubes have provided a fairly complete picture over the period October 1967 to May 1970, and have established the average differences that exist between sites both at different altitude, and at the same altitude but of different vegetation and slope. Table 11 summarises these results in terms of the average temperature for the two year period from June 1968 to May 1970, for all the sites studied, and gives similar data from other places for comparison.

TABLE 11. Average Annual Soil Temperatures (°C) at the Study Sites together with some Average, Annual Air Temperatures for comparison

Station		Average Temperature °C
Reykjavik	Iceland	3.9
2780'	Dun Fell	4.1
2700'	"	5.0
2500'	"	5.2
2050'	"	5.5
1900'	"	5.5
Above Netherhearth	Moor House	5.7
1700'	Dun Fell	5.8
Blanket Bog	Moor House	5.8
Limestone Grassland	"	5.9
1400'	Dun Fell	6.2
1200'	"	6.4
Peaty Gley	Moor House	6.4
Carecetum	"	6.4
Peaty Podsol	"	6.6
Lerwick	Shetland	7.1
Edinburgh	Scotland	8.6
Plymouth	Devon	11.0
Jersey	Channel Islands	13.1

Thus, the average temperature difference between 1200' and 2780' on Great Dun Fell is 2.3°C, while a difference of 1.1°C, almost half the Dun Fell range, exists between the Podsol and Above Netherhearth sites, both at about 1800'. To place these average temperatures in perspective it may be noted that a difference of 2.4°C exists between the annual average temperatures of Plymouth and Edinburgh.

The Podsol site, at 6.6°C, is the warmest of all the sites under study, its southerly slope and well drained soil being most important here, but it is nonetheless colder than the coldest sea-level station in Britain, namely Lerwick. It is also twice as cold as Britain's warmest sea-level station which is Jersey with an average temperature of 13.1°C. The comparison between 2780' and Reykjavik is particularly close. These comparisons must not be taken too far as the values quoted for the distant stations are those for air temperature and not, as has been measured on the nature reserve, ground temperatures.

It has been noted earlier that the temperature differences between sites are not consistent; rather, that during winter and spring there is a tendency for these differences to be minimised, and during summer and autumn divergences of temperatures occurs. Any attempt to explain fully this and other effects would require that additional climate measurements, such as windspeed, sunshine, and rainfall, had been made at the study sites; clearly beyond the scope of this work. However, it is worthwhile noting that it is particularly in the summer and autumn that differences in vegetation height and density mainly manifest themselves, and could perhaps be expected to produce greater differences in soil temperatures under the prevailing conditions of sunshine and wind. With some exceptions discussed earlier, the temperature divergence in summer and autumn does not alter the relative positions of the Dun Fell sites on the temperature scale. At Moor House the differences

are less distinct. However, over the period December 1969 to March 1970 the Blanket Bog became some 0.9°C warmer than the Podsol. During much of this time both the Bog and the adjacent Peaty Gley site were covered by a snow drift, while the Podsol was not. The insulating effect of the snow could be responsible for the warmer Bog temperature on this occasion.

It has been my experience that the amount of snowfall gave little indication about snow depth on the moor. It was necessary to know the direction and speed of the wind prevailing at the time of the snowfall and afterwards, to gain some idea of where drifts might have formed. This irregular accumulation of snow could have considerable effect on the soil temperatures, especially where a period of hard frost follows the snowfall.

The temperatures have been considered so far purely as physical measurements of the study sites. The biological significance, that is, the effect on mortality, growth, and time of moulting, pupation, and emergence, will be discussed more fully in a later section. Some indication of the biologically significant differences in relation to crane-flies can be obtained by calculating cumulative day-degrees over the annual life cycle of the insects. It is assumed for the present purpose that temperatures below 0°C produce no detectable change in dry weight and these temperatures are all accordingly considered as 0°C, and so do not contribute any increase

in a calculation of day-degrees. A series of day-degree values for the period 23.5.68 to 9.6.69 are presented in Table 12, and illustrated in Figure 10.

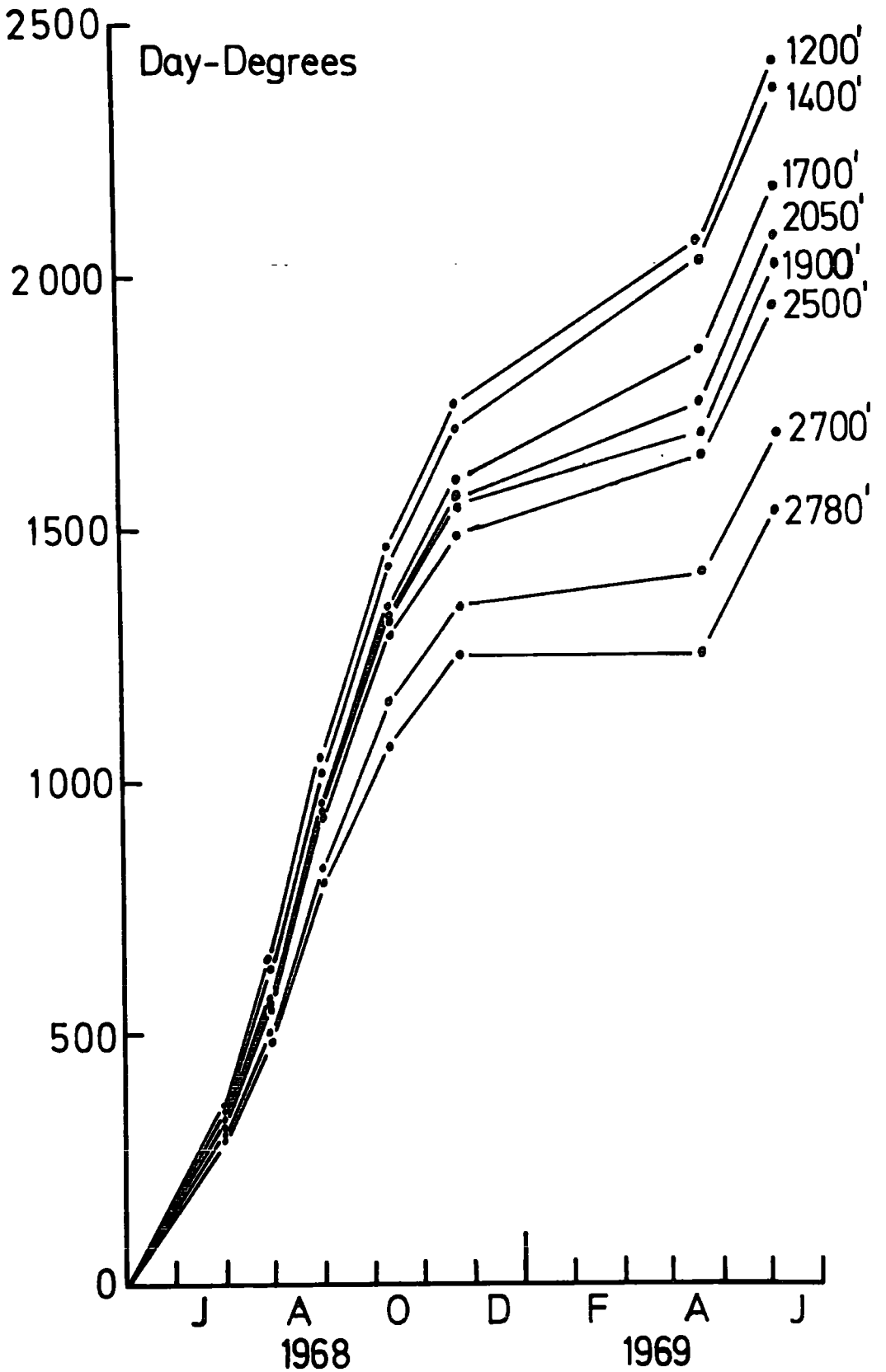
TABLE 12. Cumulative Day-Degrees above 0°C, Great Dun Fell

Dates	1200'	1400'	1700'	1900'	2050'	2500'	2700'	2780'
23. 5.68	0	0	0	0	0	0	0	0
2. 7.68	364	356	332	324	332	320	300	292
25. 7.68	654	625	574	559	562	550	505	488
1. 9.68	1053	1017	957	939	942	926	832	803
9.10.68	1475	1430	1349	1315	1322	1287	1158	1069
20.11.68	1752	1695	1592	1546	1545	1485	1347	1250
21. 4.69	2073	2036	1851	1691	1753	1639	1408	1250
9. 6.69	2428	2381	2181	2016	2083	1944	1693	1525

From 23 May to the onset of the winter over 50% of the final divergence has occurred. The position of the 2050' site is seen interposed between the 1700' and 1900' sites, and the four sites 1700' to 2500' are fairly close together by 9.6.69, but are distinctly separated from 1200' - 1400', and 2700'. The convergence and divergence of temperatures, discussed earlier, has a negligible effect on the cumulative day-degree results, which are very stable both between individual sites and from year to year.

From the average annual temperature table presented earlier, a reasonably linear relationship exists between the seven Great Dun Fell sites, 1200' to 2700',

Figure 10. The cumulative day-degrees for the Dun Fell sites over the 383 day period, 23 May 1968 to 9 June 1969. Temperatures below $0^{o}C$ are all considered as $0^{o}C$ and so contribute neither an increase or a decrease to the day-degree sum.


2500
Day-Degrees
2000
1500
1000
500
0
1200'
1400'
1700'
2050'
1900'
2500'
2700'
2780'
J
A
O
D
F
A
J
1968
1969

showing a drop of 0.1°C for every 100 feet increase in altitude. The 2780' site is the only site that does not lie within this general relationship, being disproportionately colder, possibly for the reasons of greater exposure already mentioned.

4. ADULT EMERGENCE STUDIES

4.1 Introduction

The Tipulidae of the Moor House National Nature Reserve have been described by Coulson (1959, 1962), and Hadley (1966, 1969) has conducted a biological study on Molophilus ater. In the present work, adults of the latter species have been extensively studied both in the field and in the laboratory, together with subsidiary observations on several species known to be common. Attention has been given to the factors affecting the date of emergence, and the duration of emergence of the adults at sites of differing altitude or vegetation.

4.2 The Emergence Period of Molophilus ater

Introduction

Hadley has shown M.ater to be univoltine at Moor House, passing most of the year in the larval stage, which has four instars. After pupation in May, the adults emerge during late May and early June in a highly synchronised manner with the middle 67% of the emergence occurring in 5 to 7 days. He also showed that the emergence is delayed at higher altitudes, the peak emergence occurring 7 to 9 days later at 1800' than at 1500'.

It has already been shown that large temperature differences can exist over the wide altitude range on Great Dun Fell. Populations of M.ater have been found at 1400' and 2700' and at sites in between. Clearly some mechanism

must exist that enables the species to have an annual life cycle under the different temperature regimes, and to achieve such a synchronised emergence. This latter is particularly important where, as in many crane-fly species, the adults only live for a short period of time and act solely as a reproductive and dispersal phase.

4.3 Field Studies

Sampling Methods

The sampling of adult M.ater populations was designed to provide information both on the density of newly emerged adults and on the emergence pattern. As the adults of M.ater possess abbreviated wings and are flightless it is possible to determine the number emerging per unit area of habitat fairly easily, using a suction apparatus to collect adults from emergence traps. Such sampling, if carried out sufficiently frequently, also gives the required information on the pattern and timing of emergence.

Each emergence trap comprised an open cylinder of either plastic or galvanised steel, enclosing 0.05 sq.m of habitat. The height of the traps was 35cm which prevented the entry and exit of M.ater via the vegetation, and a band of sticky material, smeared around the top, inner surface of the cylinders, prevented the animals from walking in and out over the sides of the traps. Hadley concluded that the alteration in microclimate that these traps produced was negligible in the present situation, where they were placed in position only a short time before the expected beginning of the emergence. The number of

traps used at each site varied from year to year as the demands of the study changed, and this detail is given later. All the traps were positioned randomly and were secured firmly to the ground by stakes or wires; this being relatively easy to do on the Juncus squarrosus sites. On the blanket bog site it was found that with careful cutting of the Calluna, the traps could be satisfactorily positioned.

Hadley showed that almost the whole daily emergence of M.ater occured between dawn and 12.00 GMT, and, consequently, as much sampling as possible was carried out in the early afternoon. It was not always possible to visit every site at daily intervals, but during each year the large majority of sampling visits were made at no more than two day intervals to each site.

During 1967 the suction apparatus described by Hadley was used. This was a modified form of the machine described by Johnson et al (1957). It comprised a Smith's F350 centrifugal blower, powered by a 12 volt battery. The unit was contained in a suitable housing and drew in air through a flexible hose. The animals were drawn through the hose and collected in a nylon bag held in the motor housing. One advantage of this method of collection was that the larger diameter of the collecting bag, compared with that of the hose, produced a fall in air speed, and the animals were collected in the nylon bag without damage. Using this apparatus, Hadley obtained a mean sampling efficiency of 91%.

From 1968 onwards a different apparatus was used. This comprised a 'Hoover Dustette' vacuum cleaner operated at 240 volts A.C. The electricity for this machine was provided by a Honda EIV portable generator which proved to be a reliable and very useful source of mains voltage in the field. Again, air was drawn in through a flexible hose but this time the animals were trapped at the distal end of the hose, away from the machine, in a nylon bag placed inside the aperture. Collection at this distal end of the hose had the advantage that the animals did not become trapped in the water film that often formed inside the hose when damp herbage was being sampled. This was particularly important because the Hoover hose was of the plastic, concertina type that can extend considerably, and the internal ridges would trap small insects much more easily than the smooth hose used by Hadley. The much increased air speeds of the Hoover, together with the collecting position described, did produce a higher proportion of damaged insects than the former machine, but it was found to be extremely convenient to use.

In addition to the suction sampling of the study sites, a series of pitfall traps were maintained at each site to provide a check on the progress of the M.ater emergence and also to give information on the emergence of other crane-flies. There were 10 pitfall traps at each site and each comprised a jam jar sunk into the ground, so that its rim was flush with the ground surface. A weak detergent solution was placed in each jar to wet the insects and prevent them escaping. Hadley has shown that these

traps can provide accurate information on the adult emergence pattern, although the number of insects caught, depending as it does both on the activity and the density of the animals, is affected by changes in temperature.

4.4 Studies on Great Dun Fell

4.4.1 The adult emergence in 1967

During the emergence of 1967, four sites were studied on Great Dun Fell; those described as 1700', 2050', 2500', and 2700' in Section 2. At each site five emergence traps were set up in the middle of May, and these were sampled at daily or two daily intervals. The adults were placed in containers in the field and brought back to the laboratory where males and females were separated, counted, and weighed. Some females were dissected to determine the number of eggs they contained. The males and remaining females were preserved for later study.

The preponderance of males is well known amongst the Tipulidae (e.g. Barnes 1937, Hemmingsen 1956, Coulson 1962, and Freeman 1964). Hadley recorded a mean of 64% males in his studies of M.ater and discussed the matter in some detail. In the present study a similar preponderance has been found, but as there is little or no difference between the emergence times for the two sexes, the combined results are used throughout this section.

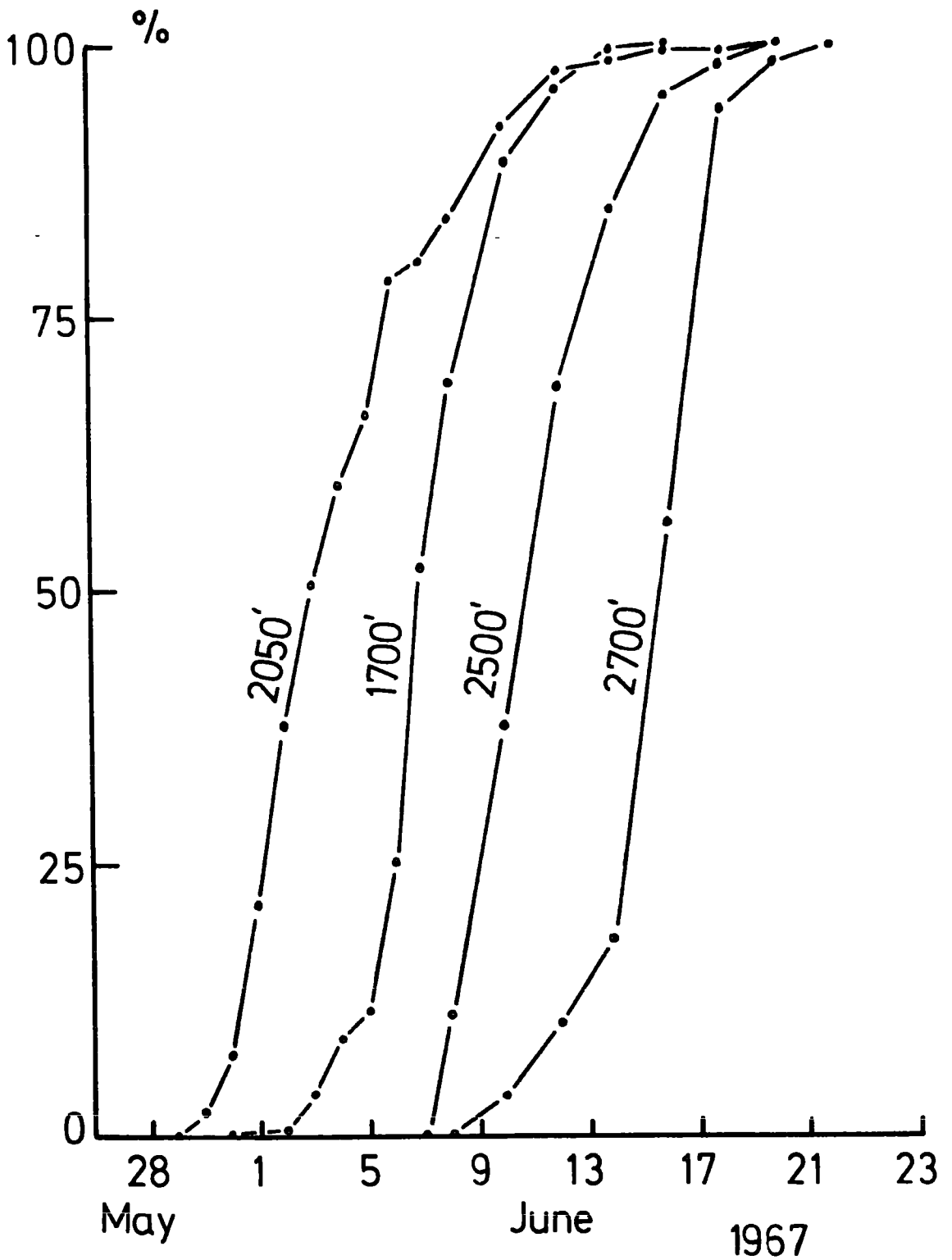
The results for the 1967 suction sampling are presented in Table 13 as the number caught on each sampling occasion. The cumulative percentage emergence from each site is illustrated in Figure 11.

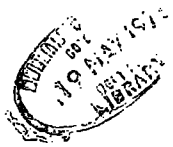
TABLE 13. The number of adults obtained from five 0.05 sq.m emergence traps, 1967

Date	1700'	2050'	2500'	2700'
May 30	0	3		
31	0	11		
June 1	1	26		
2	2	31		
3	18	25		
4	36	17		
5	16	12		
6	86	24		
7	170	1	0	
8	109	10	25	0
10	128	16	59	8
12	42	9	69	15
14	24	2	37	18
16	2	2	23	85
18	0	0	8	86
20		1	2	10
22		0	0	3
24			0	0
Totals :	634	190	223	225

The emergence pattern is very similar to that reported by Hadley. At 1700' the whole population completed its emergence within the first 16 days of June. The duration at 2500' and 2700' was shorter than this, and that at 2050' was longer. It is interesting to note that emergence began first at 2050' on 30 May, followed by 1700', 2500', and finally 2700'. The precise beginning and end of any emergence are difficult to determine as the number of insects involved is very small. However, while

Figure 11. The cumulative percentage emergence of M.ater at the 1700', 2050', 2500', and 2700' sites in 1967, using the emergence trap data.


%
100
75
50
25
0
2050'
1700'
2500'
2700'
28
May
1
5
9
June
13
17
21
23
1967



differences between the altitude sites become unclear at these extremes, the middle, peak emergence shows clearly the delay that can occur at the different sites. Table 14 gives the median and mean dates for emergence at each site, together with the standard deviation and standard error.

Thus, a difference of 13 days exists between the median dates of the first and last sites to emerge, and there is close agreement between the median and the mean values, with no evidence of a marked assymetry or skew.

The use of the median to describe the emergence pattern is, however, limited. A more satisfactory method is to calculate a mean date of emergence, to which may be attached standard deviation and standard error values, enabling statistical comparison between sites to be made. The standard deviation is useful in providing information about the spread of values either side of the mean; in this case the duration of the emergence. The standard error permits confidence limits to be placed on the mean itself.

Inspection of the standard error values in relation to the mean dates shows that these latter are clearly significantly different ($P < 0.05$ in all cases). Table 15 gives an analysis of variance for the four sites and shows that the between site variation is considerably greater than the within site variation, and that the difference is highly significant ($P < 0.001$).

TABLE 14. The median and mean dates of emergence on Dun Fell in 1967

Site	Median Date	Mean Date	Stan.Dev.	Stan.Err.	No.caught
2050'	3 June	4 June	3.8	0.3	190
1700'	7 June	8 June	2.5	0.1	634
2500'	11 June	12 June	2.7	0.2	223
2700'	16 June	16 June	2.3	0.2	225

TABLE 15. Analysis of variance for the 1967 emergence

Source of Var.	Sum of Sq.	Deg. Fr.	Mean Sq.	Var.Ratio	P
Between sites	18,328.65	3	6,109.54	818.143	0.001
Within sites	9,468.88	1,268	7.47		
Total	27,797.50	1,271			

It can be seen from Table 14 that the duration of the middle 68% of the emergence, which is estimated by one standard deviation either side of the mean, does show some decrease as the emergence is delayed. At 2050' the duration was 7.6 days and at 2700' it was 4.6 days, but the table shows that this decrease was not consistent through the other two sites.

The 1967 results clearly show some of the differences between the emergences at the different altitude sites. That 2050' preceded 1700' is not surprising with the knowledge of the temperature data that have already been presented. One possible solution to the problem of the life cycle taking the same length of time under different temperature conditions is for the insects to enter a diapause

which would last longer at the warmer stations. There is evidence, however, that diapause is absent in a number of crane-flies (Laughlin 1960, Coulson 1962) and neither Hadley nor the present writer have found any evidence of one in M.ater. As will be reported later, larvae obtained in the autumn have been cultured through the winter at temperatures of 10°C and 15°C, and pupae and adults obtained several weeks earlier than in the field.

Some answer to development taking the same length of time under different temperature conditions would be a reduction in size with increasing altitude. Mani (1961) noted that this feature is common amongst nival insects, but in the present study there has been no evidence of this. It will be shown later that the weight of newly emerged females is related to larval density, and this latter bears no relation to altitude. The mean wet weights of newly emerged males and females obtained from the 1967 emergence traps by bulk weighing are given in Table 16.

TABLE 16. Mean wet weights of newly emerged adult *Molophilus ater*, 1967

	Males		Females	
Site	No.	wt.(mg)	No.	wt.(mg)
2050'	37	0.52	26	0.90
1700'	387	0.60	122	0.66
2500'	109	0.41	33	0.84
2700'	81	0.47	16	0.78

4.4.2 The 1968 Transfer experiment

This experiment was devised in an attempt to provide some more information on the factors controlling adult emergence. On 23 January 1968 a series of 0.01 sq.m cores, approximately 10cm deep were taken from the 1700', 2050', and 2700' sites. The number of cores taken at each site was based on the previous month's larval population estimates so that approximately the same number of larvae were taken from each site. Some cores were replaced in the holes from which they had been taken, to act as controls, while the remainder from each site were transferred to the other two sites and replaced in similar holes there. As they were placed back in the ground each core was surrounded by a 12cm deep, cylinder of plastic, known commercially as 'Darvic'. Each plastic cylinder was positioned to project 1cm above the surface of the dense vegetation. Thus the larvae inside each soil core were isolated, and movement of larvae between the core and the surrounding soil was prevented. Appropriate care was taken in handling the cores and they were transferred as quickly as possible. The weather at the time was wet and cool.

For convenience the following nomenclature will be adopted in reference to the transfer experiment; a site to which cores were transferred will be termed a host site, while a site from which cores were taken will be termed a home site. The detail of the number of cores taken and transferred is given in Table 17.

TABLE 17. The distribution of the soil cores in the 1968 transfer experiment

Site from which cores were taken : i.e. home site	No.cores taken	No. and site to which cores were transferred : i.e. host site
1700'	20	(6 as controls (7 to 2050' (7 to 2700'
2050'	11	(3 as controls (4 to 1700' (4 to 2700'
2700'	20	(6 as controls (7 to 1700' (7 to 2700'

In May 1968, prior to the expected emergence, a further 12cm of 'Darvic' was attached to each cylinder in the ground and the upper edge covered with sticky material, as has been described for the 1967 emergence traps. Thus each core in the experiment was now surrounded by an individual emergence trap.

Emergence traps were also set up at the Great Dun Fell study sites in the same way that has been described for 1967. In 1968 five sites were studied, namely : 1700', 1900', 2050', 2500', and 2700'. At each site five 0.05 sq.m traps were used, and to avoid confusion these will be referred to as emergence traps, while the traps enclosing the 0·01 sq.m soil cores in the transfer experiment will be referred to as transfer traps.

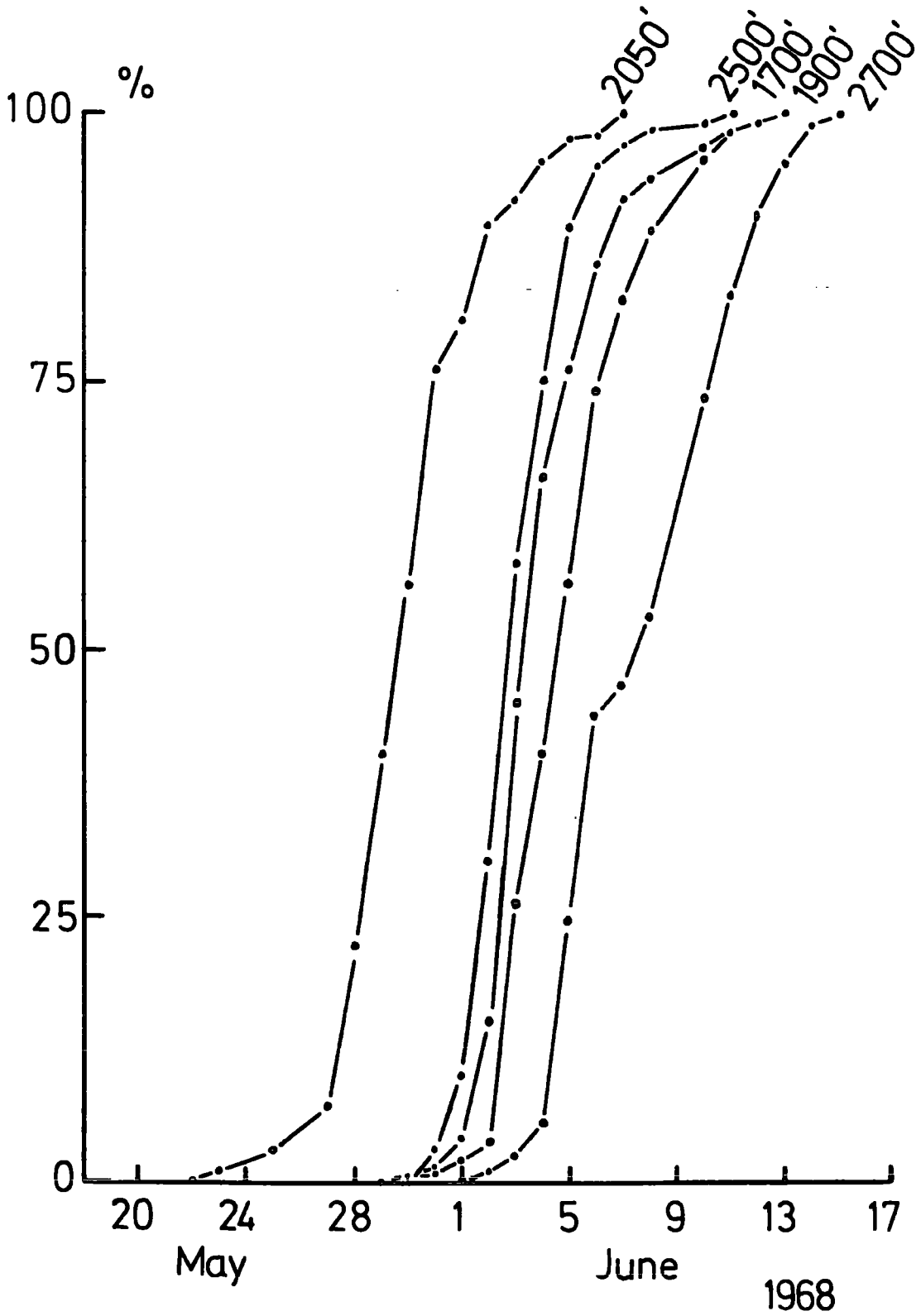
4.4.3 The Adult Emergence in 1968

The results from the emergence traps at the five study sites are given in Table 18. The cumulative percentage emergence for each site is illustrated in Figure 12.

TABLE 18. The number of adults obtained from five 0.05 sq.m emergence traps : 1968

Date	1700'	1900'	2050'	2500'	2700'
22 May			0		
23			2		
25			4		
27			8		
28			31		
29	0	0	37		
30	2	9	33	0	
31	2	1	40	8	
1 June	9	3	10	18	0
2	33	19	18	50	2
3	92	190	6	72	5
4	64	120	7	45	9
5	31	137	4	36	58
6	30	155	1	14	60
7	19	61	4	6	7
8	7	55	0	3	20
10	8	67		2	62
11	4	13		2	30
12	3	10		0	32
13	2	4			15
14	0	0			11
15					3
16					0
Totals :	306	844	205	256	304

Figure 12. The cumulative percentage emergence of M.ater at the 1700', 1900', 2050', 2500', and 2700' sites in 1968, using the emergence trap data.


%
100
75
50
25
0
2050'
2500'
1700'
1900'
2700'
20
24
28
1
5
9
13
17
May
June
1968

The adult emergence in 1968 was similar in pattern to that in 1967, though overall the 1968 emergence was about one week earlier. Thus, at 2050' the emergence commenced on 30 May in 1967 and on 23 May in 1968. At 2700' the dates were 10 June and 2 June respectively. The order of emergence was not the same as in 1967, for although in 1968 the 2050' site was again first and the 2700' site last, the 2500' emergence was slightly earlier than that at 1700'. In Table 19 the mean and median dates of the 1968 emergence are given.

TABLE 19. The mean dates of emergence 1968

Site	Median date	Mean date of emergence	Stan.Dev.	Stan.Err.	No.caught
2050'	30 May	30 May	2.6	0.2	205
2500'	3 June	3 June	1.8	0.1	256
1700'	3 June	4 June	2.3	0.1	306
1900'	5 June	5 June	2.5	0.1	844
2700'	7 June	8 June	3.1	0.2	304

Reference to the standard deviation values in Table 19 shows that the duration of the adult emergence in 1968 is different. In 1967 the emergence lasted longest at 2050', with the middle 68% lasting 7.6 days and progressed most quickly at 2700', with the middle 68% lasting 4.6 days. In 1968 the equivalent duration at 2050' was 5.2 days and at 2700', 6.4 days. The latter duration represented the longest in 1968, although the situation was not completely reversed with respect to 1967, as the shortest duration in 1968 was at 2500' where the middle 68% took 3.6 days.

4.4.4 The 1968 Transfer Experiment Results

The number of adults obtained from each series of transfer traps is given in Table 20, and some of these results, as cumulative percentages, are illustrated in Figure 13. As the emergence from the three series of transfer traps at 1700' was more or less identical, only the emergence from the 2050' series of traps at this altitude is shown.

TABLE 20. The numbers of adults obtained from the 1968 transfer traps

Larvae taken from	1700'			2050'			2700'	
Lar. taken to	Control	2050'	2700'	Control	1700'	2700'	2050'	Control
Date								
24 May				0				
26				2				
27				2			0	
28		0		3			4	
29	0	3		6	0		8	
30	3	3		11	4		7	
31	8	7	0	3	9	0	20	0
1 June	10	6	1	1	10	1	16	1
2	13	4	1	1	15	1	9	2
3	13	4	1	1	8	2	5	5
4	26	3	2	1	30	5	1	9
5	16	8	5	1	14	9	2	16
6	21	5	10	0	13	7	3	8
7	12	2	10	0	8	7	3	10
9	3	1	16		9	3	0	13
10	0	0	7		2	1		6
11			6		2	1		9
12			17		3	2		13
13			13		0	1		7
14			7			0		1
15			0					0
Totals :	125	46	100	56	32	40	127	78	102

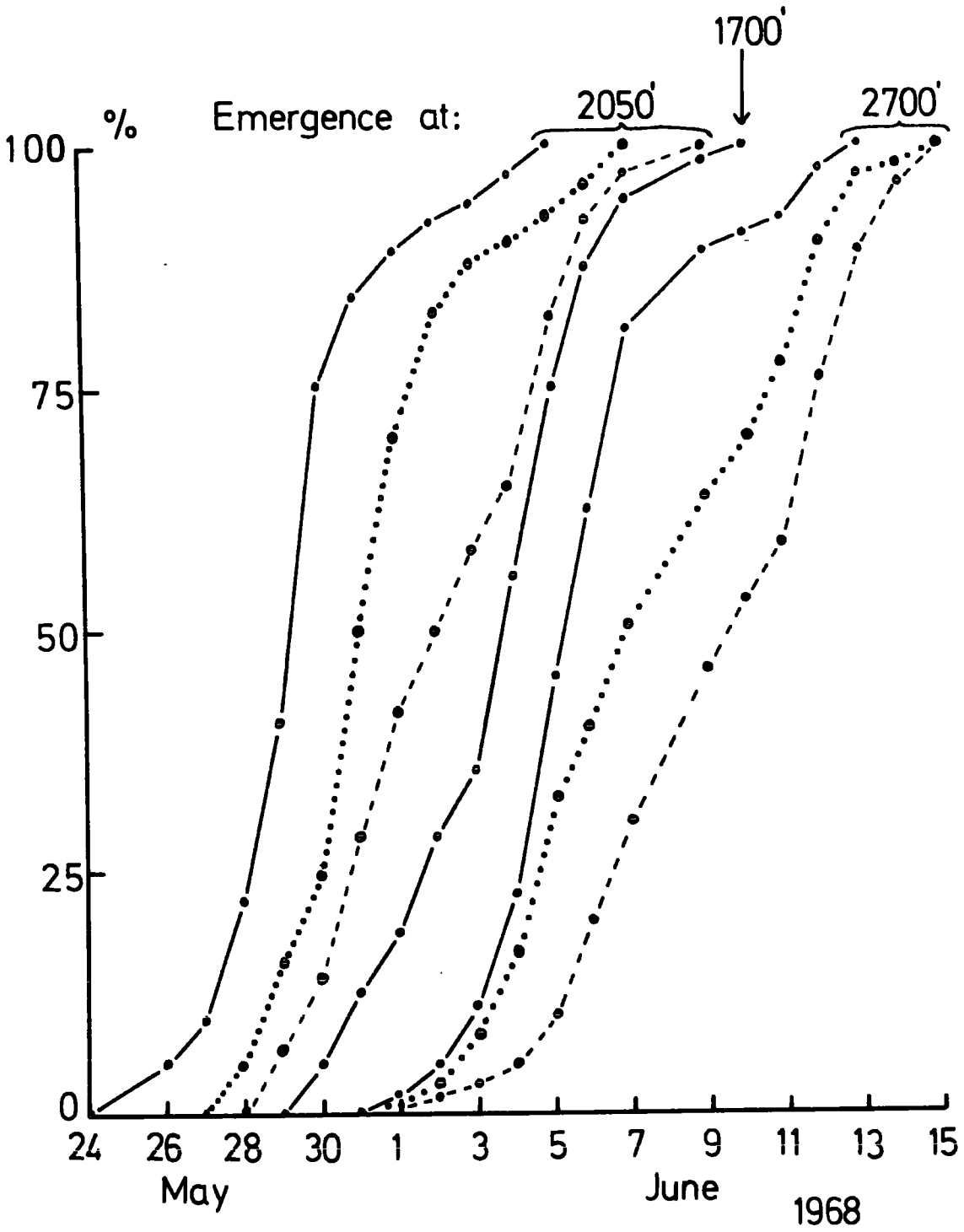
Figure 13. The cumulative percentage emergence of M.ater from the transfer traps at 1700', 2050', and 2700' in 1968.

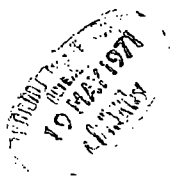
———— The emergence from larvae taken from 2050'.

-------- Tho emergence from larvae taken from 1700'.

..... The emergence from larvae taken from 2700'.

As the emergence from the three series of transfer traps at 1700' was almost identical, only the emergence from the 2050' series of traps at this altitude is shown.


1700'
Emergence at:
2050'
2700'
%
100
75
50
25
0
24
26
28
30
1
3
5
7
9
11
13
15
May
June
1968



The mean dates for the transfer trap emergences are presented in Table 21.

TABLE 21. Mean date of emergence from transfer experiment 1968

Site from which cores taken	Site to which cores transferred	Mean date	S.D.	S.E.	No. adults
2050'	Control	30 May	2.3	0.4	32
"	1700'	4 June	2.5	0.3	56
"	2700'	6 June	2.7	0.4	40
1700'	2050'	3 June	2.8	0.4	46
"	Control	4 June	2.3	0.2	125
"	2700'	10 June	3.3	0.3	100
2700'	2050'	1 June	2.4	0.3	78
"	1700'	4 June	3.0	0.3	127
"	Control	8 June	3.5	0.3	102

Before any consideration of these results it is necessary to compare the emergence of the transfer trap controls with the adult emergence at the same site, as recorded by the standard emergence traps. This is to indicate whether the transfer traps have so altered the microclimate of the transferred larvae, compared with that of the surrounding site, that the results presented above are not valid. This comparison is given in Table 22.

Table 22. Comparison of the data from the emergence traps and transfer trap controls, 1968

Site	Mean emer.date from emer.trap results	Mean emer.date from transfer trap results	d	P
2050'	30 May	30 May	1.11	0.216
1700'	4 June	4 June	1.68	0.097
2700'	8 June	8 June	0.83	0.283

The values of d have been obtained using the decimal day number that is calculated, before being expressed as the day of the month in the tables.

The table shows that no significant difference exists between the emergences recorded by the two different sets of traps. It is assumed, therefore, that the transfer traps do give a valid indication of how larvae behave when placed under the different climatic conditions prevailing at the host site.

Considering first the emergence of adults from larvae taken from the same site, larvae taken from 2050' produced adults first at the control site, 2050', then at 1700', where the mean date was 5 days later, and last at 2700', where the mean date was two days later than at 1700'. The same order of emergence holds true for larvae taken from 1700' and from 2700'. In all cases the emergence was first at 2050', then at 1700', and finally at 2700'. Table 23 presents analyses of variance for the three series of emergences from larvae taken from the same site.

TABLE 23. Analyses of variance for the emergence of adults at 2050', 1700', and 2700', in the transfer experiment, 1968

Source of Var.	Sum of squares	D.F.	Mean Squares	Variance ratio	P
A) LARVAE OBTAINED FROM 2050'					
Between sites	987.82	2	493.91	77.46	< 0.01
Within site	797.06	125	6.38		
Total	1,784.88	127			
B) LARVAE OBTAINED FROM 1700'					
Between sites	2,484.41	2	1,242.21	162.15	< 0.01
Within site	2,053.05	268	7.67		
Total	4,537.46	270			
C) LARVAE OBTAINED FROM 2700'					
Between sites	2,317.22	2	1,158.61	127.45	< 0.01
Within site	2,763.56	304	9.09		
Total	5,080.79	306			

It must be assumed that when the cores were taken in January, the larvae obtained from any one site were all at the same developmental stage in their annual life cycle. Thus something has acted on them since January, at the different sites to which they were transferred, to produce the significantly different emergences that are shown in Table 23.

Considering the emergence of adults at the same altitude site, that is, from larvae transferred from the other two sites, together with those acting as controls, the emergence occurred first at 2050', then at 1700', and finally at 2700'. In Table 24, analyses of variance are presented for the emergences at the three altitudes.

TABLE 24. Analyses of variance for the emergence of adults from larvae obtained from 2050', 1700', and 2700', in the transfer experiment, 1968

Source of Var.	Sum of squares	D.F.	Mean Squares	Variance ratio	P
A) THE EMERGENCE AT 2050'					
Between sites	267.37	2	133.69	21.47	<0.01
Within site	952.61	153	6.27		
Total	1,219.98	155			
B) THE EMERGENCE AT 1700'					
Between sites	8.17	2	4.08	0.59	>0.05
Within site	2,112.80	305	6.93		
Total	2,120.97	307			
C) THE EMERGENCE AT 2700'					
Between sites	392.13	2	196.06	18.39	<0.01
Within site	2,548.31	239	10.66		
Total	2,940.44	241			

At 1700' there was no significant difference between the three emergences, but at 2050' and 2700' the emergences were significantly different. Particularly interesting at these last two sites is the order of the emergence. At both sites the larvae from 2050' produced adults first, followed by adults from 2700' larvae, and finally adults from 1700' larvae. That the larvae from 2050' should produce the first adults might be expected, in view of the emergence pattern previously described, but the emergence of adults from 2700' larvae before those from 1700' larvae is more difficult to explain.

Thus far it has been shown that larvae removed during January and placed at different altitude sites, and therefore experiencing different climatic conditions, produce adults at significantly different times. Clearly no mechanism had operated prior to January to determine the time of pupation or adult emergence. Further comment on these data will be reserved until later results have been presented.

4.4.5 Emergence Studies in 1969

In early May 1969 standard emergence traps, each covering 0.05 sq.m, were again set up on the Great Dun Fell study sites (1400', 1700', 1900', 2050', 2700'). Three traps were used at each site, except 1900', where four were used.

It had been noted casually in 1968 that the emergence of Molophilus ater at 1400' occurred relatively early, and so, to extend the altitude range of the study, sampling was carried out here in 1969.

On 5 May 1969 a transfer experiment was carried out. The time was chosen as being close to the time when pupation was expected to begin in the field, and it was hoped to compare the results from this experiment with those from the transfer, about four months prior to pupation, in 1968.

Four circular sods each of surface area 0.05 sq.m and approximately 10cm deep were taken at each of the four sites : 1400', 1700', 2050', and 2700'. At each site one sod was replaced as a control, while the remainder were transferred, one to each of the other three sites.

The sods in the ground were immediately surrounded by a metal cylinder, sunk into the ground, with its upper edge containing the usual sticky material to enable it to act as a trap for the emerging Molophilus.

The Emergence Trap Results 1969

The results from the 1969 emergence traps on Great Dun Fell are given in Table 26.

TABLE 26. The number of adults obtained from the emergence traps in 1969

Date	1400'	1700'	1900'	2050'	2700'
22 May	0				
27	7				
29	14			0	
1 June	25			1	
3	20	0	0	3	
6	16	7	17	37	0
9	11	32	62	71	1
12	0	54	132	27	51
14		36	101	17	31
16		16	46	9	30
19		4	32	0	37
24		1	11		3
26		0	4		0
30			0		
Totals :	93	150	405	165	153

The mean and median dates of emergence are given in Table 27 from which it can be seen that in 1969 the emergence of Molophilus followed the same order as in previous years, and again demonstrated its synchronous

nature. The mean emergence dates for the 2050' and 1700' sites are the latest so far recorded, but that for the 2700' site corresponds with the mean date recorded here in 1967. It is more likely that the 2700' emergence in 1969 has occurred disproportionately early, reducing the difference between the 2050' and 2700' mean dates to six days. As was expected, the 1400' emergence occurred about a week in advance of the 2050' emergence.

TABLE 27. Mean dates of emergence in 1969

Site	Median date	Mean date	S.D.	S.E.	No.caught
1400'	1 June	2 June	3.8	0.4	93
2050'	8 June	9 June	3.1	0.2	165
1700'	11 June	12 June	2.9	0.2	150
1900'	12 June	13 June	3.7	0.2	405
2700'	14 June	15 June	3.0	0.2	153

4.4.6 The Transfer trap results 1969

The numbers of adults caught from the 1969 transfer traps are given in Table 28 which is divided into three parts showing the emergence at 1400', 1700', and 2700', respectively.

TABLE 28. The numbers of adults obtained from the transfer traps, 1969

Cores from	At 1400'				At 1700'				At 2700'			
Date	Control	1700'	2050'	2700'	1400'	Control	2050'	2700'	1400'	1700'	2050'	Control
27 May	0	0	0	0								
29	7	9	0	6								
1 June	13	20	19	34								
3	6	7	2	5	0	0	0	0				
6	9	5	2	0	0	1	2	2	0	0	0	0
9	0	0	0	0	7	8	18	12	5	4	2	0
12					10	22	22	23	7	10	4	0
14					10	12	6	14	17	25	25	42
16					3	0	4	4	9	17	5	11
19					1	0	0	0	4	0	3	3
24					0	0	0	0	0	0	0	0
Totals :	35	41	23	45	31	43	52	55	42	56	39	56

The mean dates of emergence from the transfer traps at each of the three study sites are given in Table 29, together with the usual statistical parameters.

TABLE 29. The mean dates of emergence from the transfer traps, 1969

Site to which larvae were transferred	Site from which larvae were transferred	Mean date	S.D.	S.E.	No. caught
1400'	Control	2 June	2.8	0.5	35
"	1700'	1 June	2.4	0.4	41
"	2050'	2 June	1.5	0.3	23
"	2700'	1 June	1.3	0.2	45
1700'	1400'	13 June	2.5	0.5	31
"	Control	12 June	1.9	0.3	43
"	2050'	11 June	2.4	0.3	52
"	2700'	12 June	2.4	0.3	55
2700'	1400'	14 June	2.7	0.4	42
"	1700'	14 June	1.9	0.3	56
"	2050'	14 June	2.1	0.3	39
"	Control	15 June	1.3	0.2	56

There is no significant difference between the mean emergence dates recorded by the transfer trap controls and those recorded by the independent emergence traps. At 1400' $d = 0.63$, at 1700' $d = 1.11$, and at 2700' $d = 1.43$; in all three cases $P > 0.10$. There is clearly no significant difference also between the mean dates of emergence at these three sites from larvae transferred in May from elsewhere. This is an identical situation to that recorded at 1700' in 1968.

When the emergence of adults at different altitude sites from larvae obtained from the same site is considered, it is clear from the analyses of variance presented in Table 30 that the results are significantly different. This is in agreement with the 1968 findings.

TABLE 30. Analyses of variance for the mean dates of emergence of adults at 1400', 1700', and 2700', from larvae taken from the same site in May 1969

Source of Var.	Sum of squares	D.F.	Mean squares	Variance ratio	P
A) LARVAE TAKEN FROM 1400'					
Between sites	3,040.38	2	1,520.19	222.39	<0.01
Within site	710.92	104	6.84		
Total	3,751.29	106			
B) LARVAE TAKEN FROM 1700'					
Between sites	4,081.13	2	2,040.56	471.42	<0.01
Within site	593.01	137	4.33		
Total	4,674.14	139			
C) LARVAE TAKEN FROM 2050'					
Between sites	2,216.34	2	1,108.17	279.67	<0.01
Within site	427.94	108	3.96		
Total	2,644.27	110			
D) LARVAE TAKEN FROM 2700'					
Between sites	5,197.59	2	2,598.80	851.71	<0.01
Within site	466.84	153	3.05		
Total	5,664.44	155			

Thus in both 1968 and 1969 the site to which the larvae were transferred primarily determined when the adult emergence occurred. From the results presented it is clear

that in four out of six instances there was no significant difference between the transfer emergences at any one site, and in the two examples where a significant difference did exist, the order of the emergence was not the same as that recorded from the emergence trap results.

4.4.7 Emergence Studies in 1970

It was decided to repeat the transfer experiment in 1970 in a more simple form. This year larvae were transferred in 0.05 sq.m circular sods as was described for 1969 and the method of enclosing them was identical. However, larvae were only transferred to the 1400' site from the three other sites involved in the experiment, namely, 1700', 2050', and 2700'. On each of the four occasions when a transfer to 1400' was made, two sods were removed from the 1700' and 2050' sites. At 2700' frozen ground prevented any transfer from here during the first two occasions, so it was only possible to make two transfers from this altitude, when, again, two sods were taken. At the same time that the transfer sods were taken, a further two sods were dug up and replaced as controls, as has been described for 1969. Similarly, two sods were dug up and replaced at 1400'. The details of the 1970 transfer are summarised in Table 31.

TABLE 31. Details of the 1970 transfer experiment

Date of Transfer	Sites from which two 0.05 sq.m sods were transferred to 1400'		
19 April	1700'	2050'	
29	1700'	2050'	
5 May	1700'	2050'	2700'
13	1700'	2050'	2700'

In view of the close correspondence in the past between the emergence trap results and those of the transfer trap controls, at any one site, it was decided that the control traps at 1400', 1700', 2050', and 2700' could be relied upon to provide satisfactory information about the emergence at their respective sites, and so no separate emergence traps were operated in 1970 at these sites. Two 0.05 sq.m emergence traps were employed at 1900' to give some indication of the emergence pattern at this site.

The Adult emergence in 1970

The mean dates of emergence from the five altitude sites are given in Table 32, together with the usual statistical parameters.

TABLE 32. The mean dates of emergence, 1970

Site	Median Date	Mean Date	S.D.	S.E.	No.caught
1400'	28 May	28 May	2.4	0.1	295
2050'	5 June	5 June	2.7	0.3	405
1700'	6 June	6 June	1.8	0.1	394
1900'	7 June	8 June	1.8	0.1	268
2700'	13 June	14 June	1.8	0.2	148

The emergence in 1970 clearly followed the usual pattern, although the range between the first and last mean dates, 17 days, is increased compared with 1969, when it was 13 days.

4.4.8 The results of Transfer Experiment in 1970

The emergence of adults from larvae transferred to 1400' is presented in Table 33. As there is clearly no significant difference between the mean dates for the different transfer occasions from the same altitude site, the results for the different transfer occasions have been combined and are presented in this form in Table 34.

TABLE 33. The mean emergence dates of adults at 1400' from larvae transferred on different occasions, 1970

Site from which larvae were transferred	Date of Transfer	Mean Date	S.D.	S.E.	No. caught
1700'	19 April	1 June	3.6	0.5	44
"	29 April	1 June	2.7	0.3	90
"	5 May	31 May	3.8	0.4	117
"	13 May	1 June	4.3	0.4	118
2050'	19 April	29 May	2.6	0.3	58
"	29 April	30 May	2.5	0.4	36
"	5 May	30 May	2.3	0.2	143
"	13 May	30 May	2.3	0.3	65
2700'	5 May	28 May	3.2	0.4	77
"	13 May	29 May	2.1	0.2	80

TABLE 34. Mean emergence dates of adults at 1400' using the combined data of Table 33

Site from which larvae were transferred	Mean Date	S.D.	S.E.	No. caught
1400 (Control)	28 May	2.4	0.1	295
1700'	1 June	3.7	0.2	369
2050'	30 May	2.4	0.1	302
2700'	29 May	2.4	0.2	157

While the mean dates of emergence from the transferred sods differ from the mean date of the ordinary 1400' emergence, it is clear that the emergences from the 1700', 2050', and 2700' sods has occurred much earlier than that from the control traps at the respective altitude sites. Thus the mean date for the 1700' sods at 1400' was 1st June, three days later than the ordinary 1400' emergence, but five days earlier than the control emergence at 1700'. Similarly, the 2050' sods at 1400' were two days later than the 1400' control emergence, but six days earlier than the 2050' control emergence, and the 2700' sods at 1400' were one day later than the 1400' control but fifteen days earlier than the 2700' control emergence.

Also important here is the order of emergence at 1400'. Unlike that occurring normally at the different study sites, which in 1970 was 1400' first, then 2050', 1700', 1900', and finally 2700', the order of the transfer emergence at 1400' was 1400' first, then 2700', 2050', and finally 1700'. Under these circumstances it is reasonable to assume that once again the emergence from the transferred cores was still primarily determined by the host site.

4.5 Preliminary Discussion

It is clear, from the information that has been presented and is summarised in Table 35, that each year the order of emergence of Molophilus ater adults at the different altitude sites is mostly the same. Considering the main sites, emergence commenced first at 1400', and was followed by 2050', 1700', and 1900',

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with the emergence last at 2700'. Measured in the form of mean date of emergence, the greatest delay between 2050' and 2700' was in 1967, when it was twelve days, and the shortest was in 1969 when it was six days. The emergence at 1400' occurred about one week earlier than at 2050' in the last two years of the study. The difference of five days in the 2050' to 2700' delay between 1967 and 1969 is large and ought to be explainable when some idea of the mechanism controlling emergence is known.

An equally important aspect of the emergence is its synchrony. In the majority of instances the middle 68% of the emergence lasts for less than one week. As has been said earlier, this synchrony is important in a flightless and short-lived insect, such as M.ater, if mating is to be successfully accomplished.

Table 35 shows that there is no relationship between the duration of the middle 68% of the emergence and the altitude of the site, nor is there any particular tendency for one site consistently to produce emergences of shorter or longer duration. Mani (1962, 1968), discussing the entomology of the Himalayas, noted that most species were univoltine, with adults appearing at the same time. He also found that peak emergence was delayed at higher altitudes and its duration was reduced. Mani's observations concerned altitudes some six times higher than those in the present study, but it is nonetheless interesting to note some of the similarities shown by M.ater.

TABLE 35. The mean dates and the duration (days) of the middle 68% of the adult emergences of M.ater at the main Dun Fell Sites 1967-70

Year	1400' Mean date	1400' Duration	1700' Mean date	1700' Duration	1900' Mean date	1900' Duration	2050' Mean date	2050' Duration	2700' Mean date	2700' Duration
1967			8 June	5.0			4 June	7.6	16 June	4.6
1968			4 June	4.6	5 June	5.0	30 May	5.2	8 June	6.2
1969	2 June	7.6	12 June	5.8	13 June	7.4	9 June	6.2	15 June	6.0
1970	28 May	4.8	6 June	3.6	8 June	3.6	5 June	5.4	14 June	3.6

If the development of the larvae and their subsequent pupation and emergence were a direct reflection of the temperature differences at the study sites, then the emergence pattern should have some relationship to the temperatures which the larvae have undergone.

Wigglesworth (1953) has summarised the different relationships that have been postulated to exist between the rate of insect development and temperature, and stated that, allowing for departures at the upper and lower limits, a linear relationship between the developmental rate and temperature holds for the larval and pupal development of many Diptera. The results from two series of culture studies, using fourth instar larvae, support this conclusion for M.ater.

Larvae extracted from soil samples were introduced on to agar plates similar to those used by Springett (1964), and maintained at four constant temperatures, namely 8, 10, 12, and 15°C. On 12 March 1968 samples were taken from an area of Juncus squarrosus near to the Peaty Gley site, and on 25 April 1968 from the 2050' site on Great Dun Fell. The mean number of days taken to pupation are given in Table 36.

TABLE 36. Mean number of days to pupation at different culture temperatures

Culture temp. °C	No. pupae	Mean days to pupation	S.E.
A) LARVAE OBTAINED ON 12 MARCH 1968 FROM GLEY SITE			
8	10	48	0.8
10	10	36	0.8
12	11	29	0.9
15	13	25	0.9
B) LARVAE OBTAINED ON 25 APRIL 1968 FROM 2050' SITE			
8	11	19	0.2
10	10	15	1.4
12	14	13	0.2
15	13	10	0.9

The rates of development, expressed as the reciprocal of the number of days to pupation, are plotted against the temperature in Figure 14, and in each case a linear relationship is indicated. The equations of the lines are :

March larvae $y = 0.71 + 2.67x$

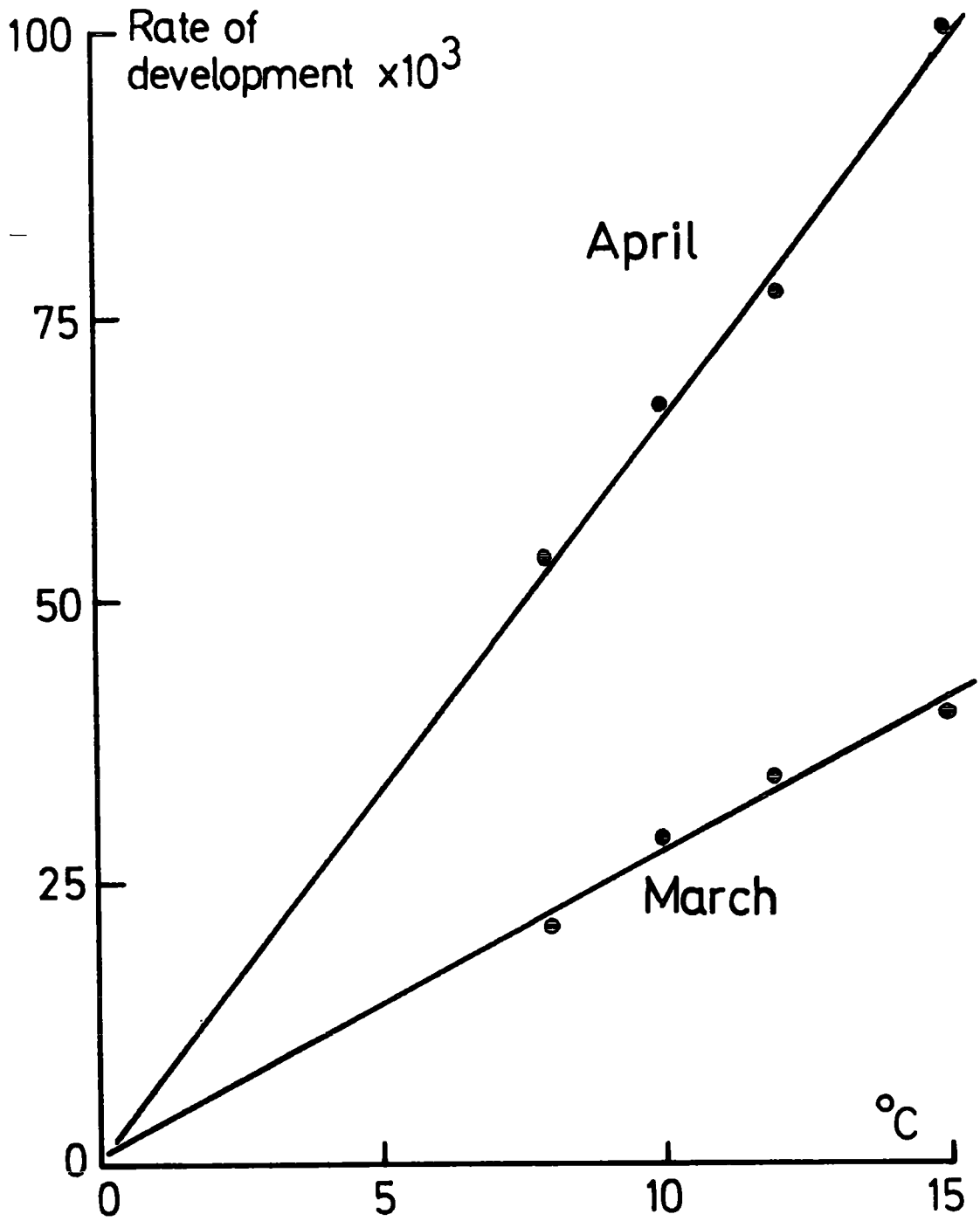
April larvae $y = 0.45 + 6.56x$

The values of x when y = 0 represent the threshold below which larval development ceases. These values are $-0.27^{\circ}C$ and $-0.07^{\circ}C$ respectively, and from these the developmental threshold for fourth instar M.ater larvae may be considered to be $0^{\circ}C$. Mani (1968), whose figures are partially revised from the 1961 work, quotes examples of aquatic Diptera developing normally at temperatures down to $-1.5^{\circ}C$.

Figure 14. The rates of larval development, expressed as the reciprocal of the number of days to pupation x 10^3, are plotted against the culture temperatures. The equations of the two lines are :

March larvae $y = 0.71 + 2.67\ x$

April larvae $y = 0.45 + 6.56\ x$


100
Rate of development x10^3
75
50
25
0
April
March
°C
0
5
10
15

The value of 0°C for the developmental threshold of M.ater larvae also agrees with the observations that it is only above this temperature that the larvae move when disturbed.

However, developmental threshold values must be interpreted with caution. It is likely that at a temperature just above the calculated threshold value, the rate of development ceases to be linearly related to temperature (Uvarov 1931), and that the true theshold is somewhat lower than that recorded here. At these temperatures, though, the rate becomes so reduced that for practical purposes the present calculation is acceptable. Further, the relationship has been calculated from constant temperature studies, and both Uvarov (1931) and Wigglesworth (1953) note that a fluctuating temperature, as found in the field, can stimulate development in excess of what would be expected, solely from a consideration of the temperature conditions.

Given the linear relationship demonstrated above, and the practical developmental threshold value of 0°C, the development of M.ater might be expected to bear some relation to the cumulative day-degree sum of those temperatures above 0°C through the annual life cycle. Such a day-degree table has already been presented in Section 3 for the 1968-1969 life cycle, and the same information, using the sucrose inversion temperatures, is given for 1969-1970 in Table 37.

It is important to note here that the temperatures used for the day-degree calculation are mean temperatures for the period of the sucrose exposure, and that a mean value of below 0°C does not preclude the temperature being above this threshold for some period during the exposure. However, the ground temperature is shown by the thermograph record not to fluctuate excessively, and it is thought that these mean temperatures can be used, with caution, to give at least a relative estimate of the annual temperature sum at the different altitude sites.

TABLE 37. The cumulative number of day-degrees above 0°C for the 1969-1970 life cycle of M.ater starting 9 June 1969

Date	1400'	1700'	1900'	2050'	2700'
9. 6.69	0	0	0	0	0
22. 7.69	525	516	503	512	469
5. 8.69	725	716	688	685	637
16. 9.69	1,342	1,325	1,293	1,303	1,229
14.10.69	1,600	1,574	1,548	1,530	1,433
2.12.69	1,860	1,805	1,768	1,750	1,571
19. 4.70	1,991	1,911	1,875	1,799	1,603
13. 5.70	2,152	2,065	2,011	1,936	1,716

Clearly, if development to the adult stage was only dependent on the prevailing temperature, then the order of emergence in 1969 should be that of the day-degree sums presented in Table 12, Section 3.

This is not so, for in Table 12 the order is : 1400', 1700', 2050', 1900', 2700', which is not the same as that presented in Table 35 for the 1969 emergence. Similarly, in 1970 the expected order of emergence from the day-degree table is : 1400', 1700', 1900', 2050', 2700', which again does not agree with the order of emergence reported in Table 35, and the number of day-degrees accumulated at 2700' over the period of the life cycle of M.ater is reached at the lower sites by November.

The results from the transfer experiments have been presented in detail and show that the timing of the emergence can be greatly altered by putting larvae under the different climate regimes that pertain at other altitude sites. When larvae are transferred to another site, the subsequently emerging adults follow the timing of the control emergence at their host site much more closely than that of the emergence at their home site. As the only main variable between the sites in this context is temperature, this is considered to be acting in some way to determine the emergence time. Of particular interest is the ability of the host site to have a large influence on the timing of the emergence, irrespective of whether the larvae were transferred to it in January, or May, immediately prior to pupation. It would be quite reasonable to argue that larvae transferred in January were either delayed or accelerated in their development rate, depending on whether they were transferred

to a site warmer or colder than their own, and that this subsequently had an effect on the timing of the adult stage. This argument, however, becomes less convincing when the results from 1969 and 1970 are considered. Here, larvae were transferred in late April and early May, times so close to the expected onset of pupation that differential development rates cannot explain the results obtained.

A hypothesis with which none of the results would conflict is that by the beginning of May the larvae at all the altitude sites have completed their development and are only inhibited from pupating by the temperature at their site being below a threshold value. This threshold value is passed first at 1400' and last at 2700' and thus the emergence sequence is determined. Larvae taken down to 1400' from 2700' in early May are therefore quite capable of pupating under the temperatures that prevail at 1400', but those remaining at 2700' are delayed until the warmer temperatures reach that altitude.

It is implied above that the threshold acts on the initiation of pupation rather than emergence. The onset of pupation in the field is difficult to determine. In their first few days the pupae are very delicate, about 4mm in length, and difficult to obtain from the soil. However, pupation can be noted to occur indirectly by the decrease of larval numbers in the soil. Once this occurred at each site, adult emergence began after about 15 days.

More direct information, both on pupation and the effects of temperature, has been obtained from culture studies which will be described now before any further discussion of this topic.

4.6 Culture Studies

It has been mentioned earlier that the culture method used was not dissimilar in any important way from that described by Springett (1964). On pupation the individuals were transferred and kept separately on pieces of damp filter paper in glass phials. The results presented in Table 38 show the mean pupation dates for larvae from a series of soil samples taken on Great Dun Fell in 1967 and 1968.

The results show the close correspondence between the pupation dates of larvae from the different sites and clearly indicate that what variation there is in the results is too small to account for the delay of 6 to 12 days that can exist between the mean emergence dates at the 2050' and 2700' sites in the field. It is reasonable to assume that some mechanism comes into operation after these cultures were initiated, to determine emergence dates, and that this is responsible for most of the variation that is recorded.

No photoperiodic effect on pupation could be detected; pupae were obtained equally well from culture plates kept in continuous light, continuous dark, and a varying photoperiod.

TABLE 38. Mean pupation dates of larvae from Great Dun Fell soil samples

Culture temp.°C	Date soil samples were taken	Site	Mean days to pupation	S.E.	No. pupae
15	8 April 1967	1700'	14	0.9	19
15	8 April 1967	2050'	14	0.9	22
15	8 April 1967	2500'	15	1.2	11
15	8 April 1967	2700'	16	0.9	20
10	10 March 1967	1700'	31	0.8	9
10	10 March 1967	2050'	32	0.8	10
10	10 March 1967	2700'	29	0.8	17
8	8 April 1967	2050'	29	0.9	11
8	8 April 1967	2700'	27	0.4	15
15	25 April 1968	1700'	15	0.4	12
15	25 April 1968	2050'	10	0.9	13
15	25 April 1968	2500'	13	0.2	11
15	25 April 1968	2700'	14	0.2	14
10	25 April 1968	1900'	21	0.7	6
10	25 April 1968	2050'	15	1.4	10
10	25 April 1968	2500'	18	0.5	9
10	25 April 1968	2700'	18	0.6	10

Some indication that a threshold temperature for pupation does exist is provided by the results from larvae cultured at 4, 6, 10, and 15°C in 1967. The larvae were obtained from soil samples taken from the study sites during February 1967, and the results which are presented in Table 39 have been obtained by combining the date for the different sites and

different sampling times through February. The number of pupae obtained suggest that at around 6°C pupation is rarely possible and that at 4°C it is not possible. The two pupae that were obtained from the 6°C culture both appeared on 1 May. The cultures were inspected until the end of June by which time all the larvae had died but no more pupae were obtained. As the mean air temperature at Moor House was 2.9°C during the period February to May 1967, and the adult emergence was completed at all the sites by the end of June, any further pupae from these cultures should have appeared by this time.

TABLE 39. The number of pupae obtained from larvae, taken from Great Dun Fell in February 1967, and cultured at different temperatures

Culture temp. °C	No. larvae into culture	No. pupae obtained
15	89	43
10	28	17
6	20	2
4	20	0

In 1968 20 larvae obtained from the 1900' site on 31 March were cultured at 5°C. No pupae had been obtained by 21 June when the Great Dun Fell emergence was over. These cultures were then placed at 10°C and on 29 June, when they were next examined, two pupae were found. No other pupae were obtained.

A pupation threshold temperature has been reported for the meal moth, Ephestia, by Wigglesworth (1953). Here the formation of the pupation hormone is inhibited at low temperature (6-9°C), although growth can still occur at these temperatures. Clearly, the small numbers of larvae involved in most of the culture results render the results less than conclusive. Nonetheless, there is some evidence here for assuming that below 5-6°C pupation cannot occur, particularly in the light of the field studies. The exact nature of the threshold in M.ater is unknown but it must operate very shortly before pupation as the attempt to detect its beginning in the 1970 transfer experiment was not successful.

It is relevant here to consider the temperature data reported in Section 3 for the different altitude sites. In 1969 information is available, over the spring and summer, from the thermographs positioned at four altitude sites : 1700', 1900', 2050', and 2700'. During May 1969 soil samples were taken from the Dun Fell sites at approximately weekly intervals. The details of these will be reported later, but it may be noted here that on 20 May none of the above four sites showed any decrease in larval density. However, on 27 May a sharp drop in larval numbers at the lower altitude sites was recorded indicating that the peak of pupation took place between 20 and 27 May. From Table 3 it can be seen that over the week 17 to 24 May the highest mean temperature was at 2050' (7.1°C),

followed by 1700' (6.9°C), 1900' (6.6°C), and then 2700' (6.5°C). This is the same order as the adult emergence reported in Table 27 and is what would be expected if a pupation threshold were the controlling factor. The closeness of the 1900' temperature reported above, to that for 2700', may also account for the emergence timing at 2700', as it will be recalled that in 1969 the emergence at 2700' followed that at 1900' much more closely than in the other years of the study.

4.7 Acclimatisation and Pupation

It has been stated already that it is important for the adults of M.ater to emerge together at each site. Further, given the difference in temperatures that exist between the different altitude sites where the population has been studied, some mechanism must exist to permit an annual life cycle at all the sites. It is reasonable to assume that some degree of temperature adaptation can occur at the colder sites so that the rate of larval metabolism is not slowed down too much by the colder temperatures.

Colhoun (1960) in a study using Blatella germanica L. showed that for each 1°C decrease in temperature, 0.13°C of cold acclimation was acquired; measured as the ability to remain active. However, he thought it questionable that this slight response to cold was of any survival value. Salt (1961) has considered the mechanism of cold hardiness in insects,

but it is important to distinguish between resistance to freezing and the adaptation of the metabolic rate, although they may be related. The matter of temperature compensation throughout poikilotherms has been reviewed by Bullock (1955) who concluded that many poikilothermal animals exhibit in their metabolism or activity some degree of independence to their temperature. He quoted the classic example of Mayr (1914) who found the pulsation rate of the jellyfish, Aurellia aurita L., to be about the same in the summer at 29°C in Tortugas, in the tropical Atlantic, as at 14°C in Halifax, Nova Scotia, but found no equally striking examples among the Insecta. Bullock thought that insects may be relatively poor in their ability to compensate for temperature but that resting stages and young stages can compensate more than adult animals.

Both the transfer and culture results have indicated that from January onwards there is little detectable difference in the stage of development of the larvae. This is what might be expected if the larvae had entered a winter diapause. However, as has been reported, there is little history of this throughout the Tipulidae and in the present study larvae have been obtained in November and induced to pupate in March after culturing at 15°C. There may be a critical time around December when larvae must have reached instar four if they are to pupate and emerge the following spring, for it has been noticed that a few larvae

that were sometimes obtained still present in instar three in January have reached instar four in culture but did not pupate with the rest of the instar four larvae, and subsequently died.

The culture results suggest that a threshold temperature, below which pupation cannot occur, lies around 5-6°C. One of the problems in this study is that while the constant temperature cultures have been able to show pupation times directly, the field studies have measured adult emergence. It has not been possible to determine pupation times accurately in the field, and these have had to be calculated from the emergence data, together with the information of larval disappearance from the soil samples. However, Hadley's results, which were confirmed in the present study, showed that pupation duration was prolonged by one day for every 2.5°C fall in temperature. Given the temperature differences existing between the sites in May and June, the differences in the duration of the pupae in the field may be considered to be negligible.

Those results from the transfer experiment, where there was no significant difference between the emergences at any one site, support the observations of the culture experiments. The other transfer results are less conclusive but, with respect to these latter, two aspects are important. Firstly, the emergences at the site to which they were transferred were closer to the control emergence at that site, rather than the

control emergence at their home site. Secondly, the order of emergence at the host site was not the same as that naturally occurring on Great Dun Fell. The host site thus still had a large effect on the emergence pattern in these cases.

The hypothesis that larvae are fully developed by around the beginning of May and are only inhibited from pupating by a low temperature is attractive in providing a mechanism for the very constant timing of the Molophilus ater emergence from year to year under the different temperature conditions that can occur. It is the delayed arrival of the pupation threshold temperature, over the altitude range, that is suggested as determining the emergence sequence.

Few similar studies over an equivalent altitude range are available for comparison. That of Jordan (1958, 1962) on the rush moth, Coleophora alticolella, at Moor House, showed that egg duration and instar development were delayed at higher altitudes, but that the adult emergence showed very little difference in its timing. However, this species experiences a winter diapause, the synchronising effects of which are not available to the M.ater populations.

4.8 Comparative studies on M.ater at the Moor House Sites

Introduction

The studies on Molophilus ater at the Moor House sites have been directed primarily towards continuing the population measurements of Hadley.

However, data on the adult emergence pattern have been collected, both by suction sampling and by pitfall trapping. Some of these results are given below for a comparison with those already presented from Great Dun Fell.

Emergence Results

The numbers of adult M.ater obtained in 1967 from five 0.05 sq.m emergence traps at the Gley and Caracetum sites, and ten 0.05 sq.m traps at the Podsol site, are given in Table 40. The daily catch from the Podsol site is illustrated in Figure 15, with the cumulative percentage catch from the three sites presented in Figure 16. The latter figure also includes similar data obtained from the Blanket Bog pitfall traps.

TABLE 40. The numbers of adult M.ater obtained in 1967 from five 0.05 sq.m emergence traps

Date	Carecetum	Peaty Podsol	Peaty Gley
23 May	0		
24	1		
25	0		
26	1		
27	2	0	
28	1	1	
29	2	1	
30	3	3	
31	12	5	
1 June	6	12	
2	6	26	0
3	7	97	5
4	2	140	13
5	7	154	12
6	7	188	75
7	2	215	58
8	1	129	37
9	0	70	58
10	0	36	21
11	2	16	19
12	0	12	7
13	0	9	1
14		2	5
15		1	1
16		1	1
17		2	0
18		0	0
Totals :	62	1,120	313

Figure 15. The numbers of M.ater caught daily from five 0.05 sq.m emergence traps at the Peaty Podsol site in 1967.

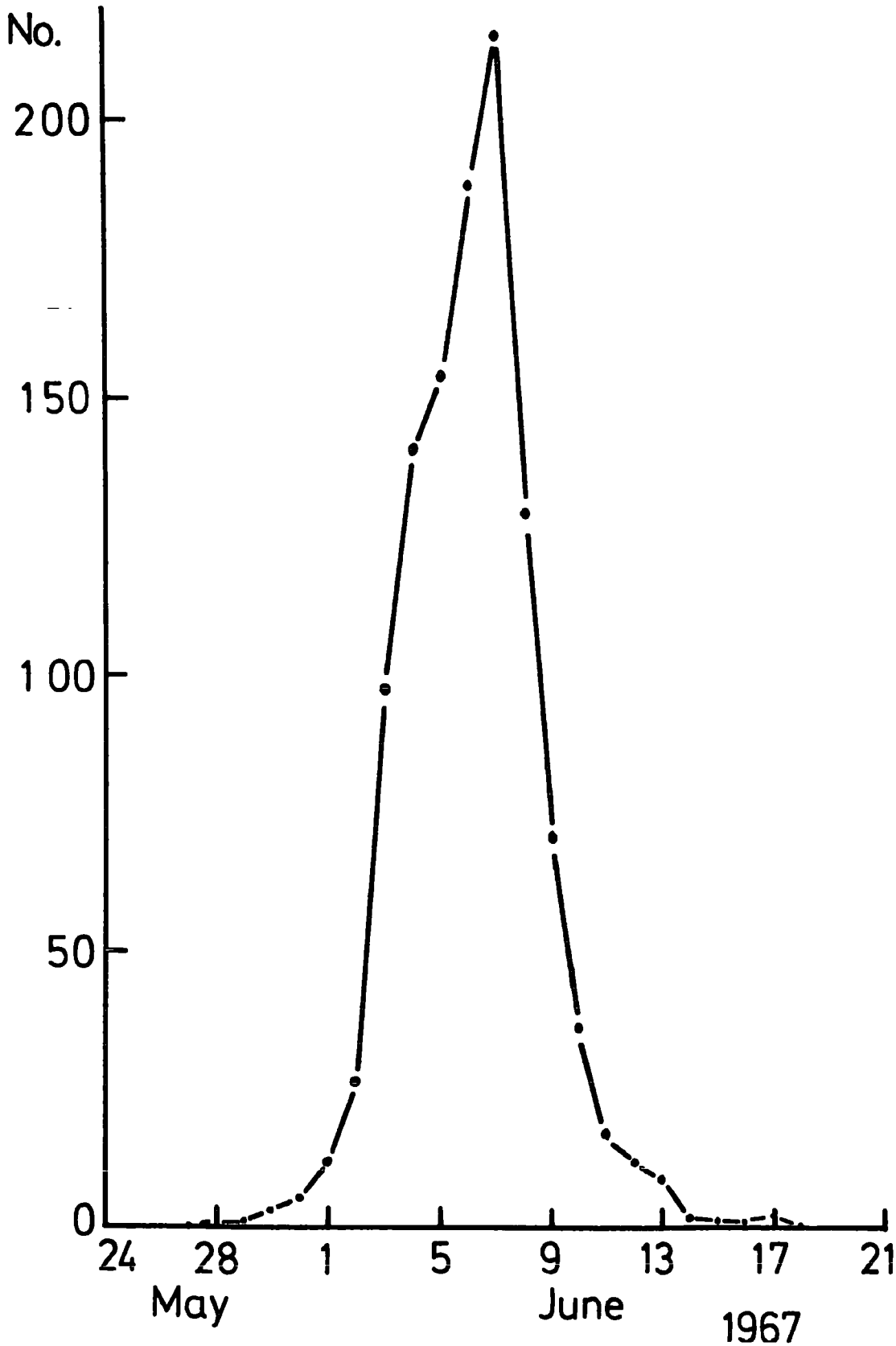
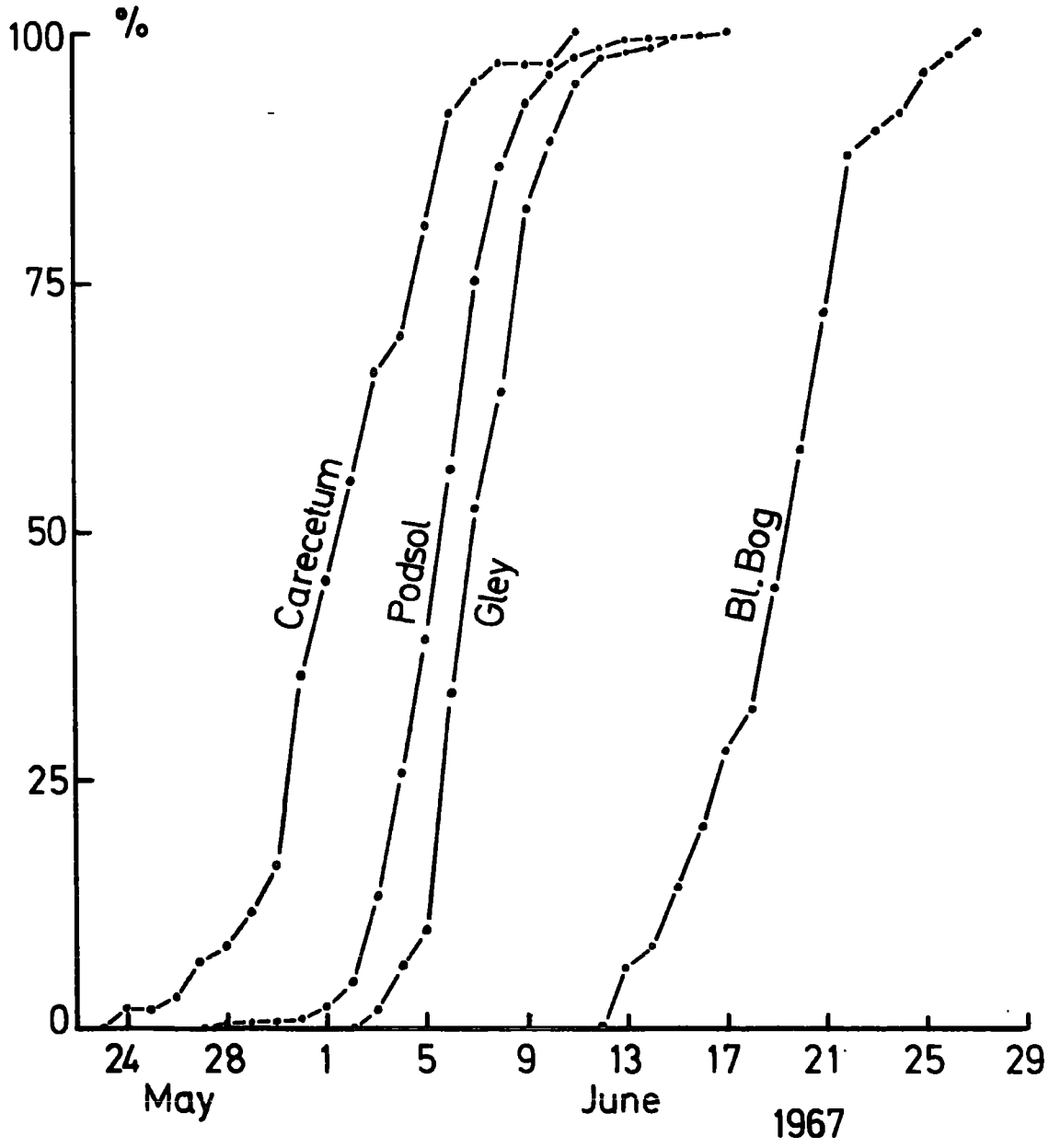

No.
200
150
100
50
0
24
28
1
5
9
13
17
21
May
June
1967

Figure 16. The cumulative percentage emergence of M.ater at the Carecetum, Peaty Podsol, Peaty Gley, and Blanket Bog sites in 1967. The details of the Blanket Bog emergence have been obtained from pitfall trap data and the details of the emergence at the other three sites from emergence trap data.


%
100
75
50
25
0
Carecetum
Podsol
Gley
Bl. Bog
24
28
1
5
9
13
17
21
25
29
May
June
1967

The mean and median dates of emergence are given in Table 41 and show the sequence of emergence to be the same as that found by Hadley, namely, Carecetum first, followed by Podsol, Gley, and finally Blanket Bog.

TABLE 41. The mean and median dates of emergence at four Moor House sites in 1967

Site	Median Date	Mean Date	S.D.	S.E.	No.adults
Carecetum	2 June	2 June	3.6	0.5	62
Peaty Podsol	6 June	6 June	2.4	0.1	1,120
Peaty Gley	7 June	8 June	2.2	0.1	313
Blanket Bog	20 June	20 June	3.3	0.5	50

It is interesting to compare the timing of this emergence from the Moor House sites, all of which are about 1800' in altitude, with that from Great Dun Fell. The mean date from the Gley site is the same as that for the 1700' site, while the mean date for the Carecetum is two days earlier than 2050', making the Carecetum site the first to produce adults of those sites studied in 1967. The mean date at the Blanket Bog site, 20 June, is relatively late, being twelve days after the Gley emergence and four days later than the mean date at 2700'.

In 1968 suction samples were taken at three Moor House sites; Peaty Podsol, Peaty Gley, and Blanket Bog. The emergence data are presented in Table 42 and show the same sequence as in 1967. The timings relative to the Great Dun Fell sites, however, are not the same as in 1967.

The Gley site in 1968 was two days later than the 1700' site and the Podsol site this year was three days earlier than the Gley, compared with two days in 1967. In 1968 the Blanket Bog emergence was only seven days later than the Gley, but its mean date of 13 June was five days later than the 2700' emergence on Great Dun Fell. Thus, overall in 1968, the Moor House emergence was later than that on Great Dun Fell, compared to 1967.

TABLE 42. The mean emergence dates for three Moor House sites in 1968

Site	Median Date	Mean Date	S.D.	S.E.	No.adults
Peaty Podsol	2 June	3 June	3.0	0.1	621
Peaty Gley	5 June	6 June	3.1	0.2	160
Blanket Bog	13 June	13 June	3.2	0.4	53

It has already been noted in Section 3 that during spring and summer the Blanket Bog temperatures were particularly colder than those at the Podsol site, and this was attributed to the much wetter nature of the Bog habitat, at a time when the Juncus sites began to dry out. It is suggested that it is this factor operating at this time of the year that produces the delay in the Bog emergence. The position of the Blanket Bog site on the average annual temperature table, presented in Section 3, would not lead one to expect this result if it were the annual temperature that determined emergence time.

Casual observation indicated that the emergence at the Carecetum site in 1968 was once again the first to occur. The warmth of this site in spring has been noted in the previous section, although when the average annual temperatures are considered it appears to be no warmer than the Gley site.

Considering both the Dun Fell and Moor House sites together, the order of emergence may be taken as : 1400', Carecetum, 2050', Podsol, 1700', Gley, 1900', 2700', and Blanket Bog. This is obviously not the order of increasing coldness that is indicated by the annual temperatures in Table 11, neither is it the order of cumulative day-degrees above $0^{\circ}C$, the developmental threshold for M.ater larvae, which, in 1968-69, was Podsol, the warmest, 1400', Gley, Carecetum, 1700', 2050', 1900', Blanket Bog, and 2700', the coldest.

The timing of the emergence is thought to be closely related to the soil temperatures that prevail immediately prior to pupation, and the thermograph records have shown that over short periods of one or two weeks the order of increasing temperature at the different sites may not always be the same as the order of the longer term, monthly or annual mean temperatures. In particular, the 1969 measurements, which were obtained over the critical period for pupation have shown the order of increasing temperature to be the same as that of the emergence at four Dun Fell sites.

Hadley (1966), in discussing the differences in the Moor House emergence, concluded that the spring temperatures at the Carecetum site could well be the warmest, and those at the Blanket Bog the coldest. He also thought that the earlier emergence of M.ater that he recorded in 1964 was due to the slightly higher temperatures recorded in the spring of that year compared with 1965. In the present study the emergence at all the sites was earliest in 1968 and latest in 1969. There was little difference between the average mean daily temperatures recorded in the Moor House meteorological screen for April and May, which were 4.3°C in 1968 and 4.2°C in 1969. However, the average maximum daily temperature was 8.4°C in 1968 and 7.9°C in 1969. In the context of the temperature threshold discussed earlier, this latter parameter may be more relevant in considering the overall effect of the climate, but the final relationship, particularly for the intermediate years of 1967 and 1970 when the average daily maximum temperatures for the same period were 7.6°C and 8.4°C respectively, between field temperature and emergence is difficult to demonstrate.

The duration of the adult emergence is affected by several parameters. Firstly, there is the time taken for the threshold temperature to penetrate the whole site and reach all the larvae. The effects of different vegetation cover have already been discussed in relation to the different microclimates that they can produce,

although there is no evidence that the site that is the most variable in this respect, the Blanket Bog, produces an emergence that is longer than the more uniform Juncus squarrosus sites. By the nature of the threshold response, the temperature differences at the different sites will be minimised during the pupation period and it has been stated earlier that a 2.5°C decrease in temperature only prolongs pupation by one day.

It is thought most likely that the duration of the adult emergence of M.ater is most closely related to the climatic conditions prevailing during the emergence itself. Both Coulson (1953) and Hadley (1966) have noted that a cold, wet day will depress the emergence, although this does not necessarily imply that it will be prolonged. No information on the effect of temperature on emergence, or the position of the emerging pupae in the soil, which is important in this context, is available from the present study. This, together with detailed field measurements of temperature, prior to and during pupation and emergence, are worthy of further investigation.

4.9 Emergence studies on other Crane-flies

4.9.1 Tipula subnodicornis

The emergence pattern of Tipula subnodicornis, a species shown to be abundant by Coulson (1959, 1962) on the Moor House Nature Reserve, has been studied using pitfall traps on Great Dun Fell. The details of these traps have been given earlier in this section, and the

total numbers of adults caught at four sites in 1967 are given in Table 43. The males of T.subnodicornis are capable of weak flight, while the females are not, but though this results in proportionately fewer males being caught in the pitfall traps, it is though that reasonably accurate data on the emergence timing is obtained by this method.

TABLE 43. The numbers of adult Tipula subnodicornis obtained from ten pitfall traps at each site on Great Dun Fell in 1967

Date	1700'	1900'	2500'	2700'
18 May	0	0		
23	15	1	0	
30	49	143	13	
31	4	50	13	
1 June	6	60	21	
2	10	66	46	0
3	20	79	42	1
4	8	80	38	3
5	8	57	31	2
6	5	18	17	0
7	3	14	33	3
8	1	8	11	3
10	1	28	84	32
12	1	4	47	80
14	1	8	34	66
16	2	2	6	21
20	0	2	0	4
22		1	0	2
24		0		0
Totals :	134	621	436	217

The results show a pattern similar to that found in M.ater with the emergence commencing first at 1700' and last at 2700'. Given the behaviour of the M.ater population at 2050', it would have been interesting to compare the emergence of T.subnodicornis here, but unfortunately this species is not found at this site.

In Table 44 data similar to that in the previous table are presented for the 1970 emergence period.

TABLE 44. The numbers of adult T.subnodicornis obtained from ten pitfall traps, Great Dun Fell 1970

Date	1700'	1900'	2500'	2700'
20 May	0	0		
22	4	2		
25	14	11	0	
27	19	16	3	
29	14	26	10	0
31	16	38	20	1
2 June	19	112	25	8
4	13	109	17	61
6	12	60	48	130
8	0	12	39	107
10		3	11	75
12		0	4	11
15			0	4
19				0
Totals :	111	389	177	397

The mean emergence dates for T.subnodicornis in 1967 and 1970 are given in Table 45 together with those already presented for M.ater.

In both years the T.subnodicornis emergence occurred before that of M.ater. In 1967 the lowest two sites had the mean emergence date for T.subnodicornis eight days before that of M.ater and this difference decreased to only four days at 2700'. However, in 1970, no such trend is shown, the T.subnodicornis mean dates being five or six days earlier than those of M.ater. It might be tentatively suggested that T.subnodicornis in behaving so similarly to M.ater is regulated by a similar mechanism. A lower threshold temperature for pupation could account for these results. The results from culture studies on this aspect would be particularly interesting both in relation to such a threshold and the duration of the pupation period.

TABLE 45. The mean dates of emergence for Tipula subnodicornis and Molophilus ater, Great Dun Fell 1967 and 1970

	1967		1970	
Site	T.subnodicornis	M.ater	T.subnodicornis	M.ater
1700'	31 May	8 June	31 May	6 June
1900'	2 June	*10 June	3 June	8 June
2500'	6 June	12 June	6 June	*10 June
2700'	12 June	16 June	8 June	14 June

* calculated from pitfall trap data

4.9.2 Other spring emerging crane-flies

Coulson (1956) listed those species of crane-fly, common at Moor House, in which the peak emergence occurred in May or June. Both Molophilus ater and

Tipula subnodicornis were included in this group, all seven species of which had an adult stage which lasted for 3 to 6 weeks in the field. The mean duration of the adults of this spring emerging group was 5.0 weeks.

No direct studies have been made on any other of these species, but casual observation indicated that one of them, Tricyphona immaculata Meigen, showed a delay in emergence with increasing altitude on Great Dun Fell.

In addition to the spring emerging group of crane-flies, Coulson considered the emergence of a further two groups; those in which the peak of emergence occurred in July or August, and those with the peak in September or October.

4.9.3 The emergence of Tipula paludosa

This species belongs to Coulson's second group of crane-flies and was noted by him to have an adult duration at Moor House of 10 weeks. This longer duration of the adults characterised all seven species in the summer group, whose mean duration was found by Coulson to be 10.4 weeks.

In 1967 ten pitfall traps, of the type previously described, were operated in the enclosed area of grassland known as the meadow, directly in front of Moor House itself.

It has been found throughout this study that pitfall traps do not only yield large numbers of adult crane-flies but, in addition, often capture numbers of

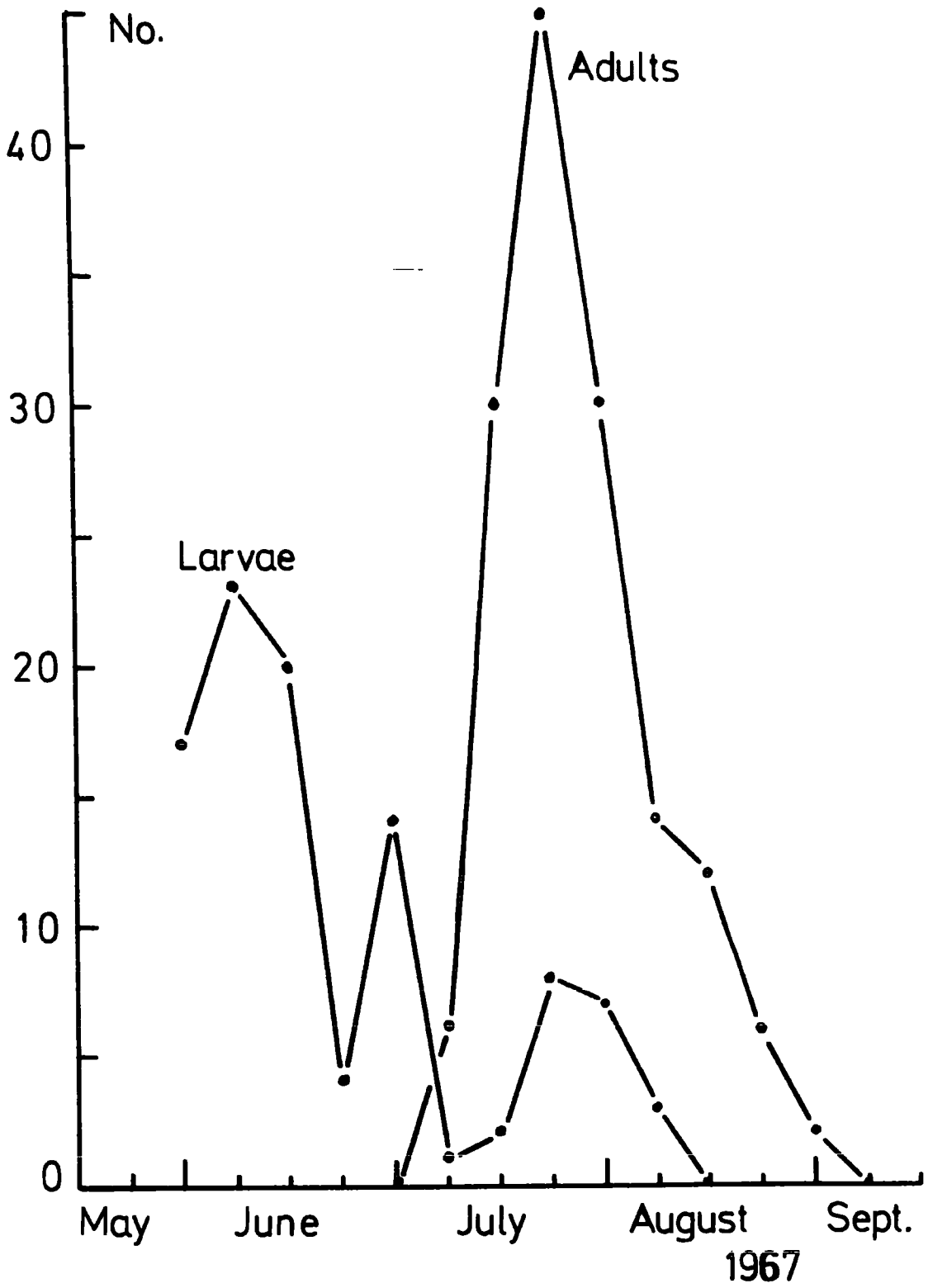
larvae of the larger species. In the cold and wet habitats that prevail on the Nature Reserve, it is not unlikely that larvae would crawl over the ground surface, and so be caught in pitfall traps.

It has been stated earlier that the results from pitfall traps must be considered with caution as the numbers that are caught are dependent not only on the density of the animal, but also on its activity. However, the results from the 1967 meadow traps are particularly interesting and are given in Table 46 and illustrated in Figure 17.

TABLE 46. The numbers of instar 4 larvae and adults of *Tipula paludosa* caught in 10 pitfall traps, Moor House Meadow 1967

Date	Instar 4 larvae	Adults
23 May		
30	17	
6 June	23	
13	20	
20	4	
27	14	0
4 July	1	6
11	2	30
18	8	45
27	7	30
1 August	3	14
8	0	12
19		5
23		2
29		0

Figure 17. The numbers of larvae and adults of *Tipula paludosa* caught in ten pitfall traps in the Moor House meadow, 1967.


No.
Adults
40
30
Larvae
20
10
0
May
June
July
August
Sept.
1967

The beginning of the adult emergence in July, and its duration of 9 weeks are more or less the same as the observations made by Coulson. Discussing the longer adult stage in the summer group as a whole, Coulson suggested that pupation was spread over a longer period of time than occurred in the spring emerging species. It is suggested here that the larval numbers obtained from the pitfall traps support this hypothesis. The data suggest that larval numbers in the soil began to decline, due to pupation, after the first week in June, and that all the larvae had pupated by the end of the second week in August. Thus pupation was occurring over a period of 9 weeks, which is the same as the duration of the adult stage. The three week delay between the beginning of pupation and the beginning of adult emergence is the same time for the duration of the pupal stage as reported by Coulson (1962).

No information has been collected for the emergence of T.paludosa on Great Dun Fell but some interesting information is available on the occurrence of T.paludosa adults throughout England. Using the results from standard Rothamsted light traps, operated in 1967, the median dates for the T.paludosa emergence at three locations are presented in Table 47, together with that for Moor House from the pitfall trap data.

TABLE 47. The median dates of Tipula Paludosa emergence at four locations in England in 1967

Site	Median date	No.of adults
Rothamsted, Herts.	15 September	144
Shardlow, S.Derbyshire	12 September	231
Durham City	19 August	126
Moor House	16 July	144

Thus the emergence of T.paludosa is delayed in warmer habitats, which is the opposite to the findings for some of the spring emerging species. Coulson suggested that in this situation the pupation of the larvae was arrested until some minimum temperature pertained in the environment. This would obviously occur earlier at higher, or more northerly, stations.

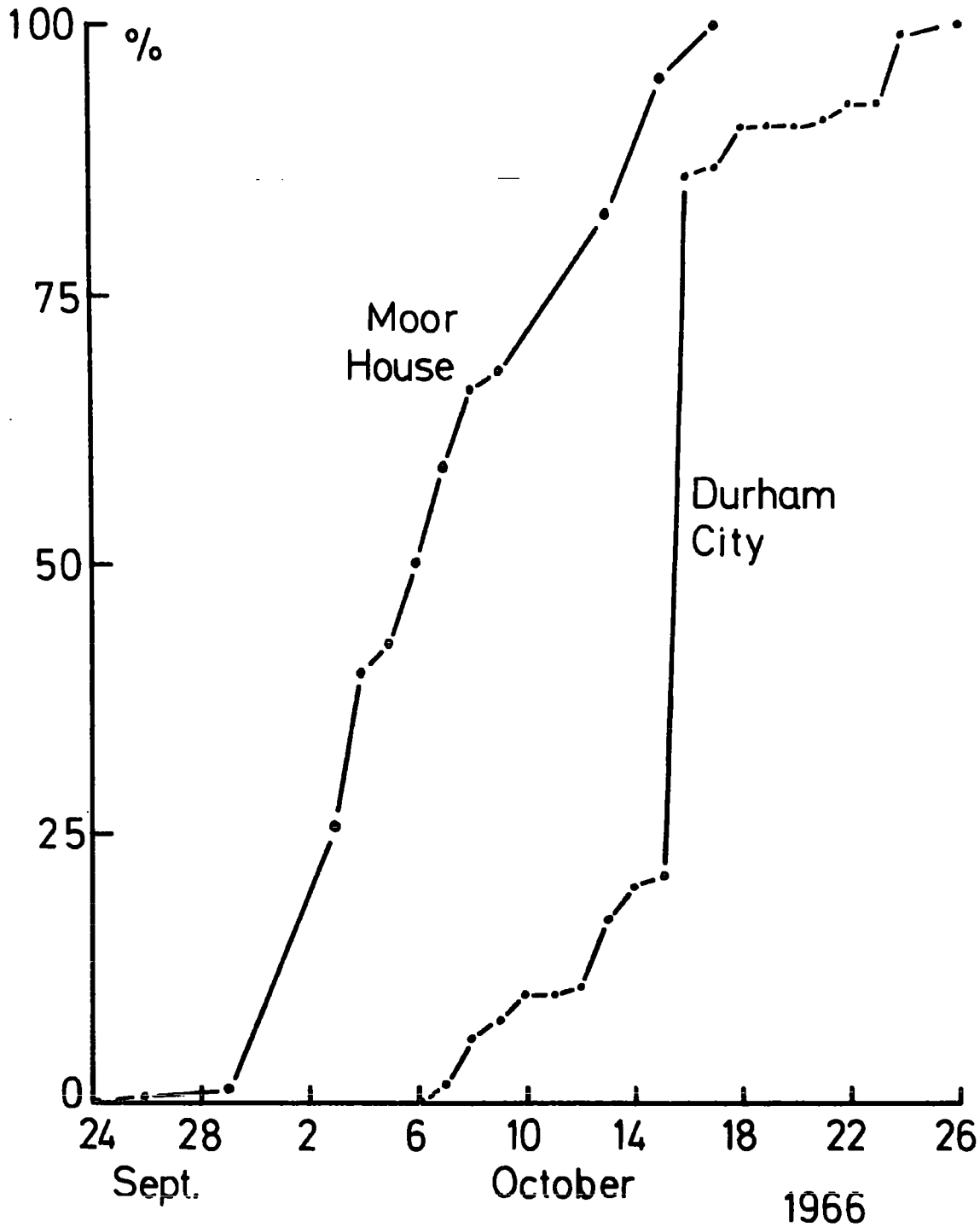
4.9.4 The emergence of Tipula pagana

Tipula pagana belongs to the third group of crane-flies; those which emerge in September or October and have a duration of the adult stage similar to that of T.subnodicornis and M.ater. The data presented in Table 48 and in Figure 18 illustrate the emergence in 1966 of T.pagana at the Limestone Grassland site at Moor House, using pitfall trap results, and at Durham City, using light trap results.

TABLE 48. The emergence of *Tipula pagana* at Moor House and Durham City, 1966

Date	No. caught in 10 pitfall traps at Moor House	No. caught in light trap at Durham City
20 September	0	
26	1	
29	4	
3 October	162	
4	94	
5	18	
6	49	0
7	55	3
8	50	9
9	5	2
10		5
11		0
12		1
13	101	12
14		5
15	81	4
16		122
17	33	1
18		7
19		1
20	0	0
21		1
22		2
23		0
24		12
25		1
26		1
27		0
Totals :	653	189

Figure 18. The cumulative percentage emergence of *Tipula pagana* from two sites in 1966; limestone grassland at Moor House (pitfall trap data) and in Durham City (light trap data).


100
%
75
50
25
0
Moor
House
Durham
City
24
28
2
6
10
14
18
22
26
Sept.
October
1966

The cumulative percentage emergence in Figure 18 clearly shows the earlier emergence at Moor House. In 1966 the median date of emergence was 6 October at Moor House, and 15-16 October at Durham City, a delay of nine to ten days. It is likely that a minimum threshold temperature for pupation could again be the controlling factor here. Casual observation has indicated that, at 2050' on Great Dun Fell, the T.pagana emergence precedes that at the Limestone Grassland site at Moor House.

4.10 Discussion

The emergence data that have been presented in this section support the grouping of adult crane-flies into the three categories that have already been described.

Detailed studies on Molophilus ater, a member of the spring emerging group, have permitted the construction of a hypothesis that will explain the control of adult emergence in this species. It would appear that cold temperature acclimation is involved in the annual life cycle, so that from January onwards no difference can be detected in the developmental stages of M.ater larvae, even though they have experienced, and will continue to experience, different temperature regimes at the different altitude sites on Great Dun Fell.

Culture studies have suggested that the cold threshold temperature for larval development lies around 0°C, though it is repeated that there are theoretical objections to the calculation of such a value. However, while larval development can continue at these low

temperatures, a quite separate threshold seems to exist for pupation. It would appear that pupation is not possible below 5-6°C. Such a threshold could take two forms.

Either a specific period, during which the temperature was consistently above 5-6°C, might be required before pupation could occur or, more likely, a given number of day-degrees would be required, above 5-6°C, to produce pupation. Thus during the increase of spring temperature, intervals when the temperature was below 5-6°C would not have any adverse effect on subsequent pupation, though they would not contribute to it either.

The observations presented for Tipula subnodicornis, also in the spring emerging group, are similar to those for M.ater, but T.subnodicornis adults occur a few days before those of M.ater in the field. It would only be necessary to postulate a lower pupation threshold to account for this.

The emergence of Tipula paludosa, a summer species in the second group, differs from that of T.subnodicornis and M.ater in two respects. Firstly, the adult stage lasts about twice as long, and, secondly, the emergence occurs earlier at colder stations. It has been suggested that a prolonged period of pupation is responsible for the prolonged adult emergence and this former may well be caused by the slower changes in the temperature at this time of the year. Thus through the spring the rate of temperature increase is rapid, but in

the summer this rate declines to zero and then begins to accelerate again, in the opposite direction, with the beginning of the autumn. This is clearly seen in Figure 5 in Section 3. It might be expected that the response to the onset of some threshold temperature would be less precise in the summer and that this would produce a prolonged pupation period.

Concerning the timing of the emergence, it has been suggested that it is necessary for the temperature to fall to some threshold value before pupation can occur. A similar situation could well apply to T.pagana, an autumn emerging species, in the third group, with the shorter duration of the adult stage due to the rapid drop in temperatures that is occurring at this time of the year.

It seems quite reasonable to assume, therefore, that despite their different behaviour, the emergence timing in the last two species is still based on the temperature control of pupation. The response to a falling temperature that seems to be shown by both T.paludosa and T.pagana has permitted them to develop adult stages during summer and autumn, obviously a useful way of avoiding competition with the spring emerging species.

It may be assumed that all those species in the spring emerging group have their pupation controlled in a similar way to that postulated for M.ater, and that all those in the autumn group behave in a similar way to T.pagana. However, it might be expected that a proportion

of the species in the summer group still responded to an increasing temperature; that is, those whose emergence occurred when temperatures were still rising, albeit slowly.

Observations on some of these summer species, and some in the other two groups, would be particularly interesting, and would provide the information required to permit the advancing of a detailed theory of emergence control in the moorland Tipulidae.

5. POPULATION STUDIES ON MOLOPHILUS ATER

Introduction

The life cycle of Molophilus ater has been described by Hadley (1966). The eggs are laid in June and hatch to the first instar larvae in approximately four weeks, and the second and third instars also take about the same length of time to develop. The over-wintering larval stage, the fourth instar, lasts from November to early May, a period of about thirty weeks, and is followed by the three week pupal phase from which the adults emerge in early June.

Throughout the present study information has been collected on the densities of the different developmental stages and this, together with related observations, is presented in this section.

5.1 The Egg Stage

The eggs of M.ater are soft and whitish with a mean length ($\pm$ S.E.) of 221 $\pm$ 9μ and mean maximum breadth of 134 $\pm$ 2μ (Hadley 1966). Several attempts, using a sieving and flotation technique, to determine the numbers of eggs in the soil after the adult emergences, were unsuccessful, although counts of the larger and more robust eggs of Tipula subnodicornis were not difficult. It is thought that the soft chorion of the M.ater eggs was responsible for their breaking up under the extraction technique.

Thus, no direct measurements of egg density have been possible and nothing is known of the timing or causes of mortality during the egg stage. The values of egg density that are used later in this section have been derived from a knowledge of the density of adult females and their fecundity.

5.2 The larval stages

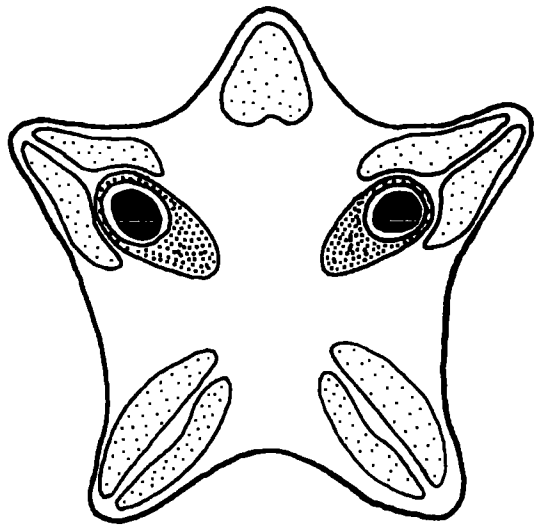
The larvae of Molophilus ater, which are very similar to the larvae of M.hirtipennis (O.S) described by Alexander (1920), are yellow-brown in colour, about 8mm long and 0.5mm in diameter. The body is noticeably constricted before the spiracular disc, whose markings are illustrated in Diagram 1. The darkly pigmented areas of the disc to the inside of the spiracles, together with the undivided area of pigmentation on the dorsal lobe, are the characteristic features of M.ater larvae. Coulson (1956) noted that the structure and the spiracular disc pigmentation of some first instar Tipulinae larvae was different from the subsequent instars, but this is not the case with M.ater whose first instar larvae have the same pigmentation as the later stages.

It is clear that there is a basic similarity of the spiracular disc pigmentation throughout the genus Molophilus. Thus M.hirtipennis (Alexander 1920), M.obscurus Meigen (Brindle 1967), and M.ater show the same arrangement here and their separation into different species would require a most detailed

Diagram 1 A The spiracular disc of a fourth instar larva of *Molophilus ater*.

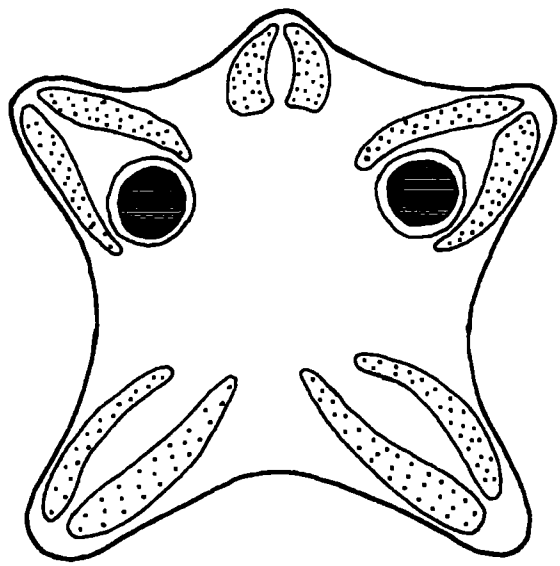
B The spiracular disc of a fourth instar larva of the genus *Ormosia*.

C The spiracular disc of a fourth instar larva of the genus *Erioptera*.



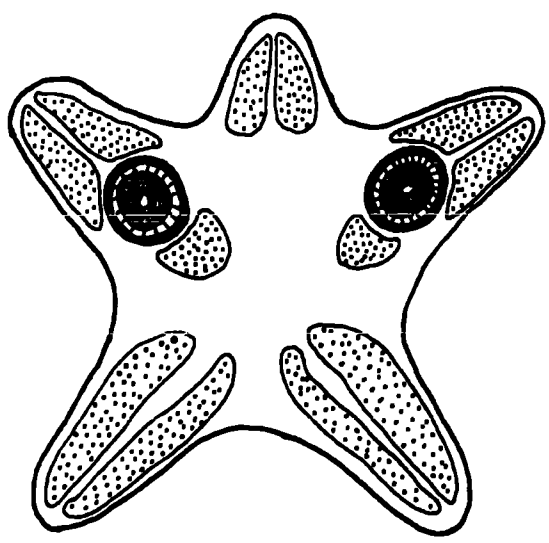
A

x 175



B

x 300



C

x 175

and careful study. However, no adult representative of the genus Molophilus, other than M.ater, has ever been found on the reserve by the present writer or by Hadley (1966), though Coulson (1956) found one adult female specimen of this genus which was probably M.griseus Meigen. Thus the problem of the identification of the larvae, to species level, has not occurred in the present study.

When soil samples were taken from both the Moor House and Dun Fell study sites several genera of small tipulid larvae were obtained in addition to those of M.ater. None of the others was as abundant as M.ater, the density of each genus being only 10% or less than that of the M.ater population. The key provided by Brindle (1967) facilitated the separation of some of these genera. Although no work is available for the species identification of the British Limoniinae, the investigations of Coulson (1959) clearly indicate which species are abundant at Moor House on the Juncus squarrosus and Blanket Bog areas, and it may be assumed that it is to these species that the majority of these larvae belong. The details of these larvae are summarised below :

Tricyphona immaculata Meigen

Larger than M.ater and bearing only two lobes on the anal segment. Four welts present on the ventral body surface.

Limnophila Macquart sens.lat.

Larger than M.ater and easily distinguished by their yellow or yellowish-brown pubescence which often imparted an irredescent effect to the cuticle.

Ormosia pseudosimilis Lundstroem

Similar in size and general appearance to M.ater but having no pigmented spot to the inner side of the spiracles (Diagram 1).

Erioptera spp. Meigen

Broader than M.ater and with the pigmented spot on the dorsal lobe divided medially (Diagram 1).

5.3 Obtaining larvae

Introduction

Throughout the study period soil samples have been taken from the different sites at intervals of one to two months. A method of stratified random sampling (Yates & Finney 1942, Healy 1962) has been employed with the site divided into a series of equal subdivisions and one soil core taken randomly from within each. The cores were initially taken to a depth of 9cm but subsequently it was found that only rarely were larvae obtained below a depth of 6cm and cores of this depth were then used. The larvae of M.ater may well descend deeper into the soil profile during periods when the ground is frozen, but it has not been possible to take any samples under these conditions.

Care was exercised throughout to ensure that the core was subjected to the minimum of vertical compression, and the soil corers that were used were all of a design that produced no lateral compression.

The soil cores were returned to the laboratory in plastic trays and stored prior to extraction, at a temperature close to that prevailing on the Nature Reserve.

Previous experience (Hadley 1966) showed that a dynamic extraction process, using the wet funnel method developed by O'Connor (1955, 1962) was best suited for the extraction of M.ater larvae. In this method heat is applied from a shaded light bulb to the soil, which is spread on a sieve, and submerged in a funnel filled with water. The larvae, in moving away from the heat source, pass downwards through the sieve, and fall through the water to be collected at the funnel base.

Lateral temperature gradients across the funnel were avoided by the close contact between the lamp shade and the top of the funnel, and the complete apparatus was operated in a draught free room of relatively constant temperature. The heat regime was controlled by changing the voltage to the light bulbs using a 'Variac' transformer.

In the first months of 1968 it became apparent that the soil sampling and extraction were not producing consistent results and an investigation into the method was initiated using an area of J.squarrosus moor adjacent to the Peaty Gley site.

5.3.1 The Sample Unit

In any comparison of sampling, different procedures must be compared on a common basis and this is frequently the amount of work involved (Southwood 1966). In the present study the size of the sample units or the number of such units to be taken were less important factors than the time taken to extract the larvae.

The importance of using a thin layer of substrate in each funnel has been stressed by Peachey (1962). Thus to limit the depth of substrate to no more than 1.5cm in each funnel it was necessary to divide each 6cm deep, 0.005 sq.m core between four funnels, while cores of 0.002 sq.m and 0.001 sq.m of similar depth were divided between only two funnels. It follows that with an extraction apparatus comprising 60 funnels, 15 soil cores of surface area 0.005 sq.m could be extracted in any one session while the number was 30 for the 0.002 and 0.001 sq.m cores.

On 12 March 1968 the following series of 6cm deep cores were taken from the previously sampled site :

15 cores of surface area 0.005 sq.m

30 cores of surface area 0.002 sq.m

30 cores of surface area 0.001 sq.m

Five of the largest cores and ten of the other two sizes were extracted on each of three occasions. The results of this comparison of sampling regimes are presented in Table 49.

TABLE 49. The densities of M.ater larvae indicated by three different sampling regimes

Size of core	No. taken	Vol.of soil per funnel cm^3	Density of larvae per m^2	Standard Error
0.005	15	75	707	172
0.002	30	60	700	123
0.001	30	30	833	131

While the mean densities are not significantly different from each other, the 0.001 sq.m cores gave the highest mean density and it is thought that this is probably due to the small amount of substrate in each funnel. However, the results provide no estimate of the efficiency of the extraction process. The introduction of a known number of larvae into sterilised soil cores, or into peat that did not support a natural population of M.ater, followed by later heat extraction, can give some information on efficiency, but it was thought unlikely that the reintroduced larvae would come to occupy natural situations in the soil, a view supported by O'Connor (1957).

5.3.2 The Extraction Regime

On 26 March 1968 ninety cores of surface area 0.001 sq.m and 6cm deep were taken from the investigation site in a stratified random way. In the laboratory the soil cores were divided into six groups, each containing fifteen cores. Five of the groups were then subjected to different heat regimes on the wet funnel extractors, and the last

group was subjected to a petrol extraction method that will be described later. After wet funnel extraction the soil from the sieves was subjected to petrol extraction. The 'Variac' settings for the five extraction regimes, each of which lasted three hours, are given in Table 50. Sixty watt light bulbs were used to supply the heat.

The temperature gradients across the soil in the funnels were measured using two mercury in glass thermometers. One was positioned at the base of the sieve and the other beneath the water surface on top of the soil. The thermometers were read at fifteen minute intervals throughout each three hour extraction. The temperatures recorded by the upper thermometer are shown in Figure 19, and the gradients across the soil in Figure 20.

TABLE 50. The voltages applied to the light bulbs under the different extraction regimes

Time (mins)	'Variac' Setting (volts)				
	1'	2	3	4	5
0	90	60	60	100	250
15	90	60	60	100	250
30	105	80	90	150	250
45	105	80	90	150	250
60	120	100	120	150	250
75	120	100	120	150	250
90	135	120	150	200	250
105	135	120	150	200	250
120	150	140	180	200	250
135	150	140	180	200	250
150	165	160	210	250	250
165	165	160	210	250	250

Figure 19. The temperatures recorded by a thermometer positioned on top of the soil surface, but beneath the water surface, in a wet funnel under the five different extraction regimes shown in Table 50.

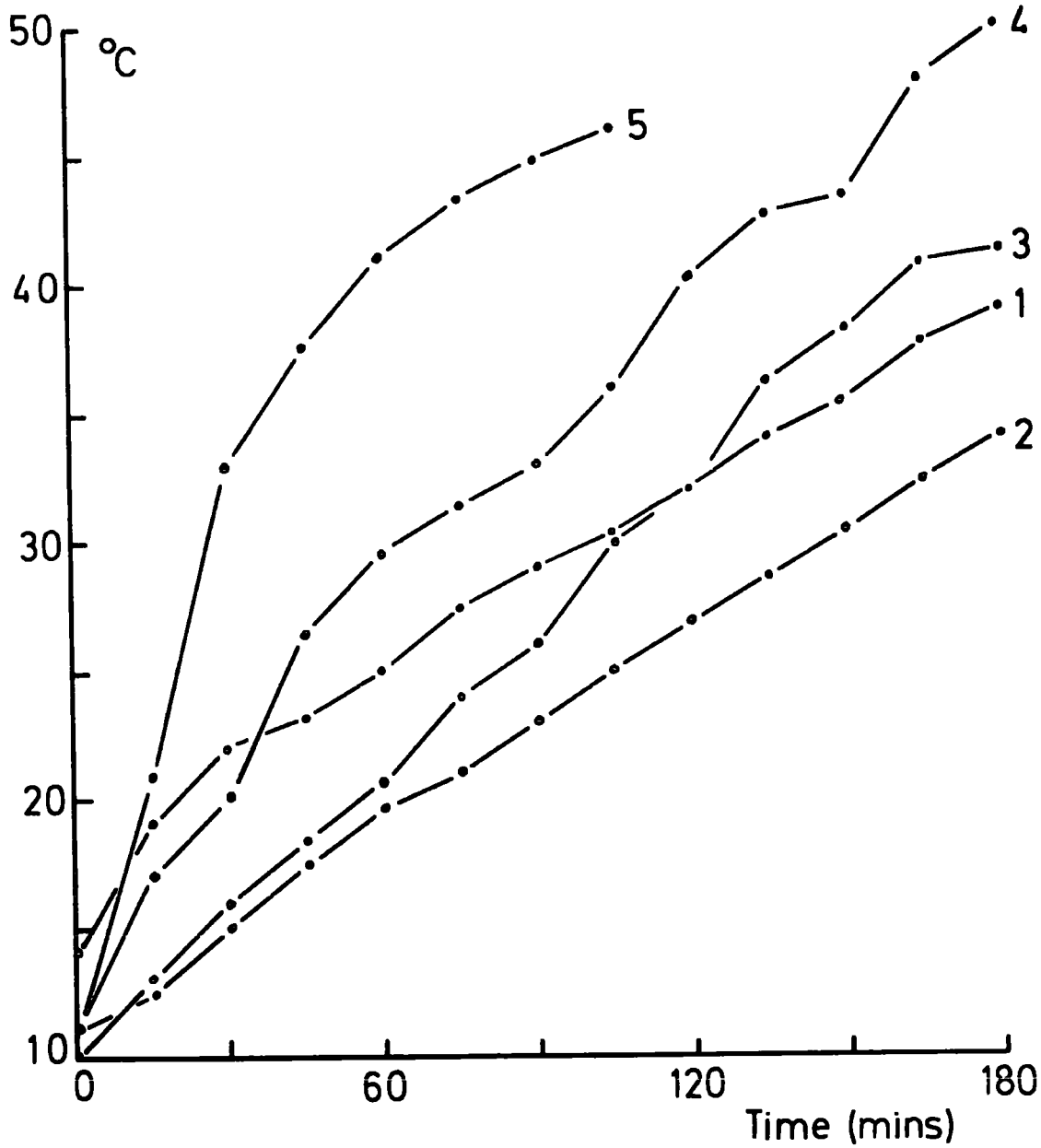
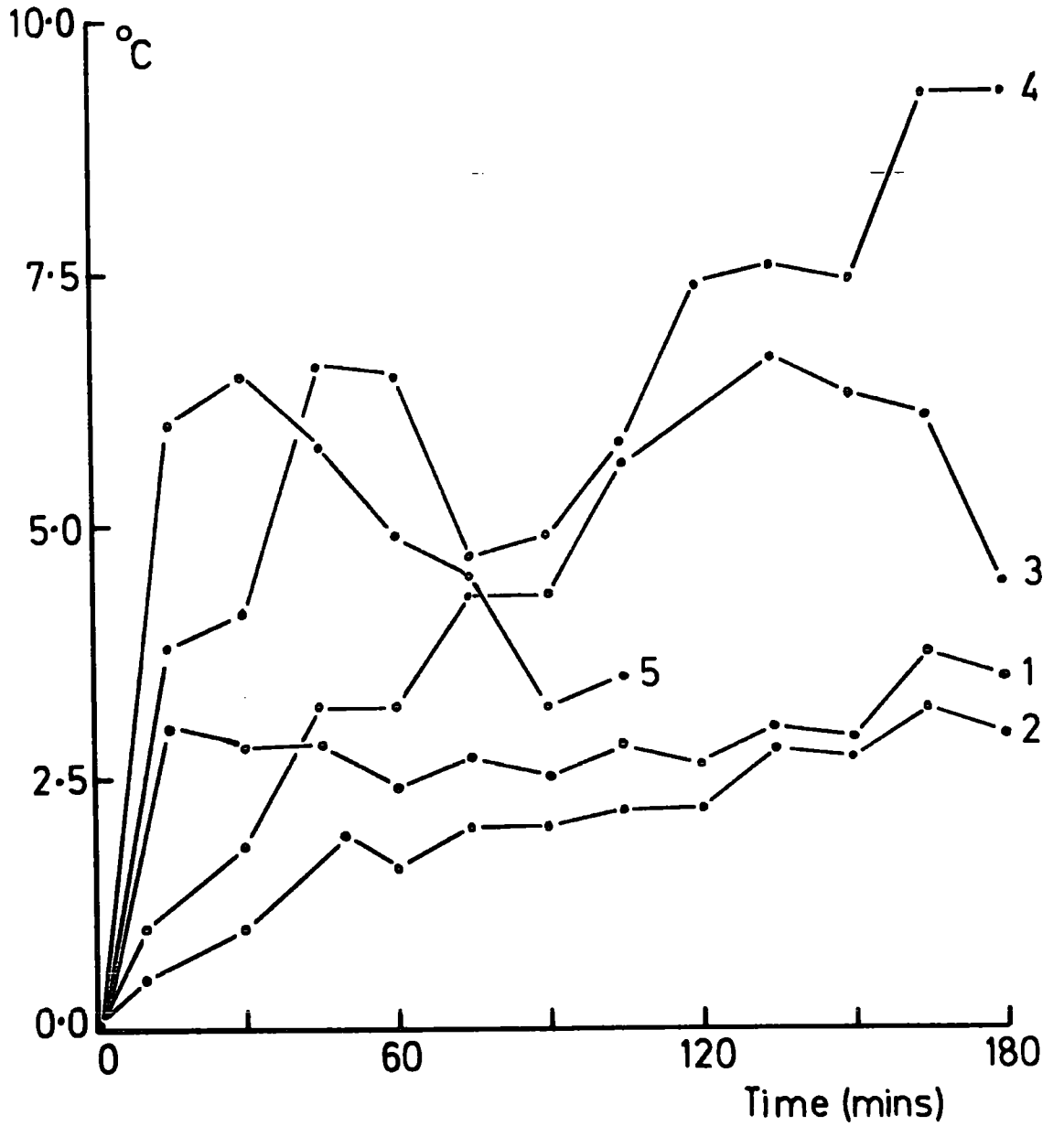

50
°C
40
30
20
10
0
60
120
180
Time (mins)
1
2
3
4
5

Figure 20. The temperature gradients across the soil in a wet funnel under the five different extraction regimes shown in Table 50.


10·0
°C
7·5
5·0
2·5
0·0
0
60
120
180
Time (mins)
4
3
5
1
2

The results from the different extraction regimes are given in Table 51. The very low efficiency of regime 5 is to be expected for the rapid increase in upper surface water, indicated in Figure 19, probably killed most of the larvae before they were able to escape from the soil. That regime 4 produced the highest efficiency is also to be expected for this regime showed a much higher temperature gradient across the soil than regimes one, two or three, without a rapid rise in the upper surface temperature.

TABLE 51. The numbers of larvae obtained from six different extraction regimes

	Wet funnel regimes					Petrol
	1	2	3	4	5	extraction
By heat extraction	10	10	10	14	6	
By petrol extraction	6	9	8	3	15	17
Total :	16	19	18	17	21	17
Efficiency of heat extraction	62.5%	52.6%	55.6%	82.4%	28.6%	

Several other factors, such as sieve size, storage of soil cores prior to extraction, and extracted larvae becoming lodged in the funnel, were tested to determine whether they involved a possible source of error, but none were found to be important.

For future larval sampling, of the later instars at least, it was decided that a sample unit size of 0.001 sq.m be used, the cores, after being divided

into two halves, to be extracted in the wet funnels under regime four. Further sampling and extraction showed that thirty sample units gave a standard error value that was about 10% of the mean number of larvae per core, at both relatively low and high densities. The density values have been corrected for the estimated efficiency of the extraction regime, and throughout the study period additional comparisons of the wet funnel extraction, with the petrol method, have confirmed that the former method has been giving satisfactory results.

5.3.3 Independent Population Estimates

The desirability of having a series of independent population estimates at the same stage has been stressed by Southwood (1966) and during this investigation two other methods were considered.

Flotation

Coulson (1962) used a solution of Magnesium Sulphate, with a specific gravity of 1,230, to float eggs of Tipula subnodicornis to the surface when the liquid was mixed with samples of soil. In the present study the large amounts of plant material present in the samples prevented any larvae being recovered by this method. Boiling under reduced pressure (Hale 1964) will wet and sink the plant material, but before this was contemplated an alternative method was tried.

Wetting the larval cuticle

Salt & Hollick (1944) originally introduced into soil fauna studies this concept of using a light hydrocarbon liquid, immiscible with water, which wets

the waxes on insect cuticle and so raises the insects to the surface hydrocarbon layer from which they can be recovered.

In the extraction of M.ater larvae using this method each core was broken into a bucket and squirted with a strong water jet. This, together with stirring, largely removed the soil from the plant roots, leaving a suspension of soil and plant material. Initially, the larger pieces of vegetation were carefully washed and removed from the bucket, but leaving them in produced no decrease in larval numbers, so this practice was discontinued.

Petrol was then poured onto the suspension in the bucket to a depth of 1cm and then the whole was agitated by blowing air up from the bottom of the bucket. This method of agitation was favoured by Salt & Hollick and in the present study was found preferable to vigorous stirring, where the petrol tended to remain as an intact surface layer, or to shaking, where the petrol could become trapped in the vegetation below the surface. Aeration produced an upwelling of the suspension through the petrol so that larvae present were retained there. It was easy to remove larvae from the petrol layer after aeration was stopped, and in all cases aeration was continued until no more larvae appeared.

It was thought that this latter method provided a satisfactory way of obtaining an independent assessment of larval population density for comparison with the wet funnel method.

Efficiency of the Petrol Extraction

A measure of the efficiency of the petrol extraction was obtained by introducing larvae into peat that did not support a natural population of M.ater. The subsequent petrol extraction of these larvae was not subject to the criticism advanced for the introduction of live larvae into sterilised cores for heat extraction. Four M.ater larvae were added to about 100cu.cm of peat with a total of eighteen replicates. Each peat sample was petrol extracted in the usual manner and from the total of 72 larvae placed in the samples, 66 were recovered, giving an extraction efficiency of 91.6%. Although this value was pleasingly high, petrol extraction could not be contemplated as the main technique owing to the amount of time required to carry it out.

5.4 Larval Development

Hadley (1966) has given measurements of the maximum diameter of the spiracular disc of M.ater which permit the instar of any larva to be easily determined. A random subsample of larvae obtained from an extraction was used to determine instar composition. The larvae were first killed in hot water and then placed vertically, with the head pointing downwards, in a container filled with small glass beads and water. The beads proved a satisfactory method for holding the larvae while the spiracular disc was being measured. Because the disc could not always be positioned exactly horizontally, precise measurements of its maximum diameter could not be obtained by this method,

but there was no difficulty in determining to which of Hadley's four distinct categories the larva belonged.

The number of larvae from each site measured after each sampling occasion varied between 20 and 60 although normally less than 20 larvae from the Blanket Bog site were measured. Larval development towards the fourth instar stage can be expressed as the mean of the instar stages present in each sample, and the data in this form are presented in Table 52 for the two seasons 1967-68 and 1968-69.

TABLE 52a. The mean instar (± S.E.) of larvae during 1967-68

i) Dun Fell Sites

Date of sample	1700'	2050'	2500'	2700'
18 July 1967	1.48 ± .10	1.57 ± .11	1.36 ± .10	1.11 ± .05
31 August	2.87 ± .04	3.16 ± .11	2.67 ± .09	2.18 ± .08
1 October	3.41 ± .05	3.63 ± .04	3.41 ± .07	3.44 ± .08
30 October	3.70 ± .11	3.82 ± .03	3.69 ± .08	3.70 ± .06
26 November	3.89 ± .04	4.00	3.91 ± .09	3.95 ± .03
14 January 1968	3.96 ± .02	4.00	3.92 ± .08	4.00
31 March	4.00	4.00	4.00	4.00

ii) Moor House Sites

Date of sample	Carecetum	Gley	Podsol	Bl.Bog
21 July 1967	1,57 ± .14	1.41 ± .08	1,45 ± .11	1.00
23 August	2.86 ± .14	2.60 ± .07	2.72 ± .06	1.53 ± .13
10 October	3.79 ± .07	3.76 ± .07	3.71 ± .04	3.22 ± .10
2 November	3.86 ± .05	3.95 ± .03	3.89 ± .03	3.78 ± .10
26 November	3.97 ± .03	3.97 ± .03	3.95 ± .02	4.00
2 January 1968	4.00	4.00	3.97 ± .02	4.00
6 April	4.00	4.00	4.00	4.00

The results from the 2050' and 2700' sites during 1967-68 are illustrated in Figure 21. The mean hatching date for each site has been estimated from a knowledge of the mean emergence date for the adults, assuming a mean duration of 24 days for the egg stage in the field, and this has been given the value of 1.0 in Figure 21.

TABLE 52b. The mean instar (± S.E.) of larvae during 1968-69

i) Dun Fell Sites

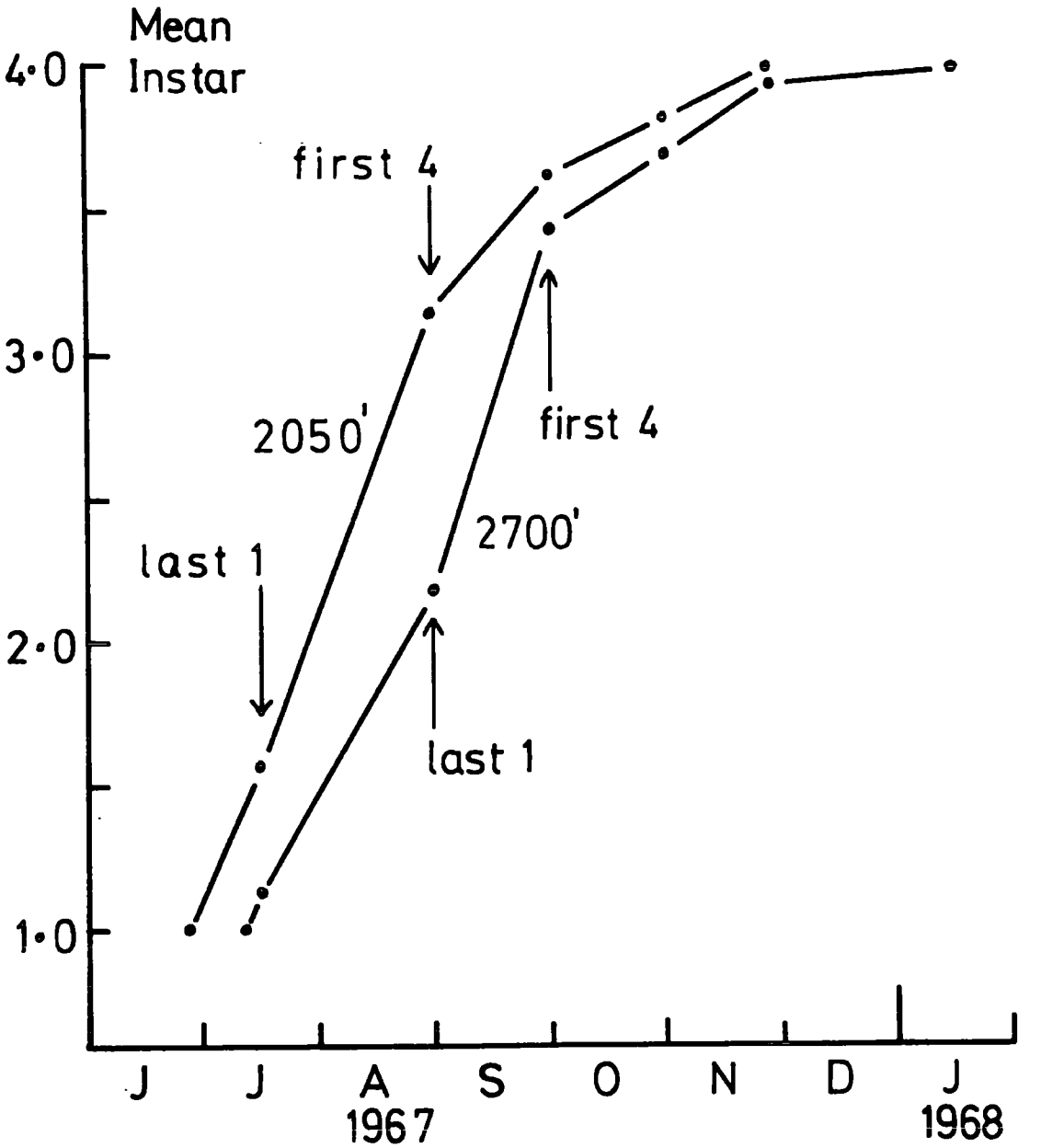
Date of sample	1400'	1700'	1900'	2050'	2500'	2700'
3 July 68	1.00	1.00	1.00	1.00	1.00	
14 July	1.31±.13	1.08±.06	1.06±.04	1.13±.09	1.10±.10	1.00
25 July	2.17±.11	1.31±.12	1.48±.11	1.50±.15	1.33±.14	1.20±.13
1 Sept	3.09±.10	2.97±.14	3.14±.09	3.03±.09	2.89±.07	2.86±.13
4 Nov	4.00	3.90±.05	3.88±.04	3.88±.06	3.97±.03	3.94±.04
21 Apr. 69	4.00	4.00	4.00	4.00	4.00	4.00

ii) Moor House Sites

	Gley	Podsol	Bl.Bog
2 July 68	1.00	1.00	
25 July	1.45±.16	1.50±.15	1.00
1 Sept	3.09±.11	3.09±.11	2.75±.31
4 Nov	3.90±.06	3.92±.04	4.00
13 Apr 69	4.00	4.00	4.00

It is appreciated that the value for the mean instar just after the estimated hatching date gives little information on the development of the larvae since all the eggs may not be hatched. Similarly, the converging of the curves in the autumn is merely the consequence of the fourth instar being the final one. However, some information on the rate of development at the different sites can be obtained by

Figure 21. The development of larvae at the 2050' and 2700' sites in 1967-68, expressed as the mean instar on each sampling occasion. The sampling dates when instar one larvae were last found and instar four larvae were first found are indicated.


Mean
Instar
4·0
3·0
2·0
1·0
first 4
2050'
last 1
2700'
first 4
last 1
J
J
A
S
O
N
D
J
1967
1968

considering the middle section, mostly covering the month of August, and in Table 53 the rate of instar development, over the time period indicated, has been expressed as the difference between the mean instar at the beginning and end of the period, divided by the number of days. The mean site temperaturesin Table 53 for 1968 are those recorded by the sucrose method and presented in Section 3. The temperatures for 1967 have been obtained by the addition of 0.4°C to the 1968 results. Records from both the Moor House and Dun Fell meteorological screens show that in August 1967 the mean air temperature was 0.4°C above that for August 1968.

The relationship between rate of development and temperature is illustrated in Figures 22 and 23 for the two years. In each figure a line for the Q_{10} relationship of 2.0 which may be taken as an average value between rate and temperature, has been drawn passing through the mean rate and mean temperature co-ordinates. In each case the slope of this line is significantly higher than that of the regression line of measured rate of development on site temperature. It is recognised that the number of observations in each figure is relatively small, and that the temperature range is also small, but there does seem to be some evidence here for the acclimatisation of developmental rate with a Q_{10} of 1.44 in 1967 and 1.07 in 1968. It has been suggested in a previous section that towards the end of the winter there is little difference in the development stages of the larvae at the different sites.

TABLE 53. The development rates of larvae and the field temperatures

i) 1967

Site	Period	Development rate per day x 10	Estimated mean site temp. °C
1700'	18.7-31.8	0.316	10.5
2050'	"	0.361	10.4
2500'	"	0.298	10.3
2700'	"	0.345	- 9.0
Carecetum	21.7-23.8	0.391	12.0
Gley	"	0.361	12.6
Podsol	"	0.385	12.1
Bl.Bog	"	0.352	11.2

ii) 1968

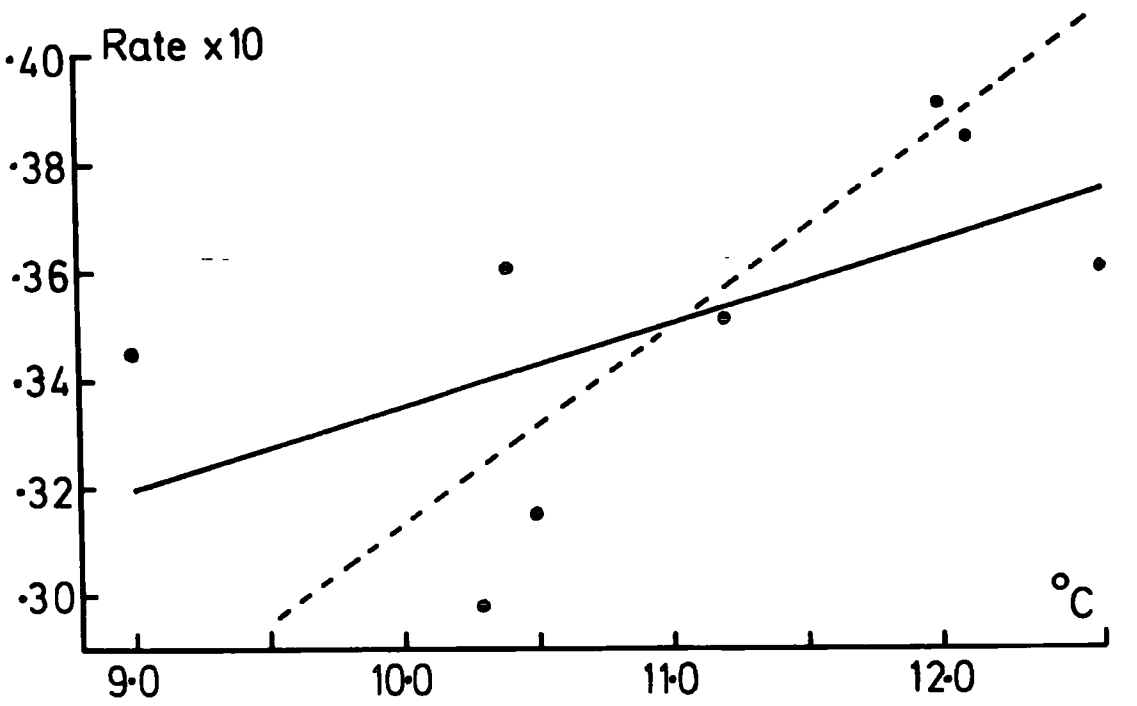
1400'	14.7-1.9	0.363	10.6
1700'	25.7-1.9	0.437	10.1
1900'	"	0.437	10.0
2050'	"	0.403	10.0
2500'	"	0.411	9.9
2700'	"	0.437	8.6
Gley	"	0.432	12.2
Podsol	"	0.418	11.7
Bl.Bog	"	0.461	10.8

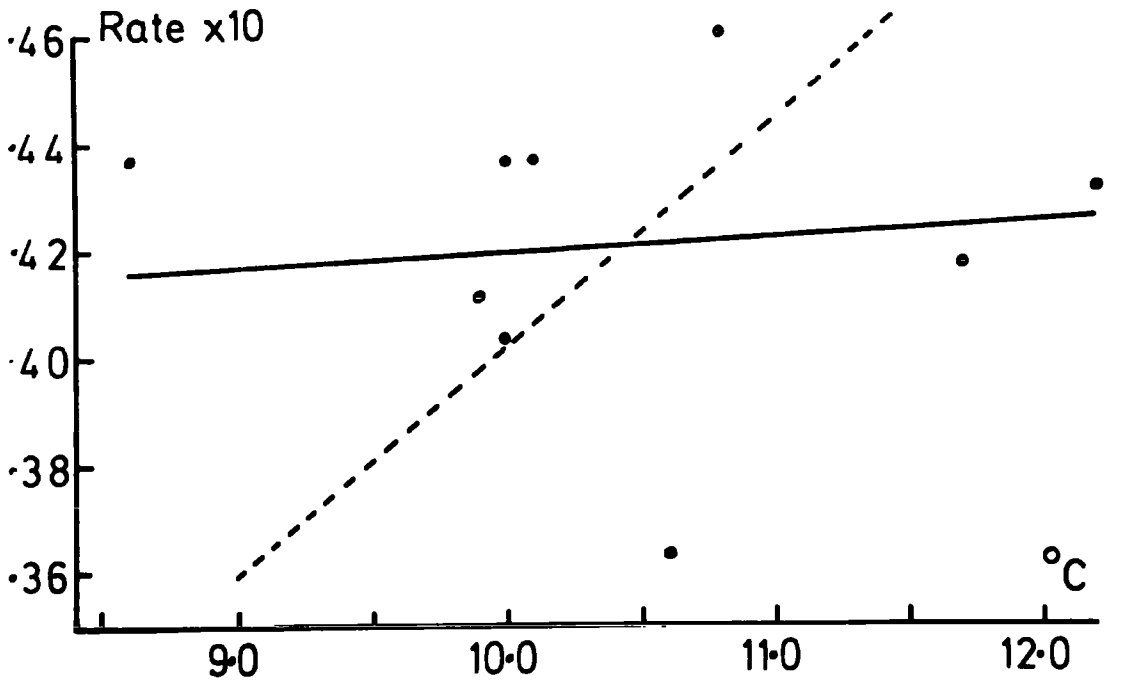
The low Q_{10} values obtained above would minimise the effects of temperature differences towards this end. Controlled laboratory studies of early instar larvae in culture at different temperatures would provide more conclusive evidence about the relationship between developmental rate and temperature.

Although considerable variation exists between the development rates at different sites, it is clear that

Figure 22. The development rates of M.ater larvae at the different sites during the summer of 1967 in relation to the site temperatures. The equation of the regression line is $y = 0.179 + 0.0156\ x$. For comparison a line representing the Q_{10} relationship of 2.0 has been drawn passing through the mean rate and mean temperature coordinates.

Figure 23. The development rates of M.ater larvae at the different sites during the summer of 1968 in relation to the site temperatures. The equation of the regression line is $y = 0.390 + 0.003\ x$. For comparison a line representing the Q_{10} relationship of 2.0 has been drawn, passing through the mean rate and mean temperature coordinates.


Rate x10
·40
·38
·36
·34
·32
·30
°C
9·0
10·0
11·0
12·0


Rate x10
·46
·44
·42
·40
·38
·36
°C
9·0
10·0
11·0
12·0

overall the 1967 values are lower than those for 1968. In 1968 the mean rate of development for the seven sites common to both seasons was 8.1% higher than that for 1967. It is possible to construct a minimum temperature hypothesis for some change, possibly from instar two to three; so that in the warmer year this change is delayed, with the resulting reduction in the developmental rate measured over this period, but a convincing explanation must await more information from the studies mentioned earlier.

5.5 Measurement of Weight and Fecundity

Larval Weight

During 1967 and 1968 mean live weights of M.ater larvae, obtained from the study sites, were recorded. Larvae from each site were weighed collectively on a sensitive electro-microbalance after having the excess water on their cuticles removed by rolling them on filter paper. The weighing was accomplished as quickly as possible to minimise further desiccation losses. The mean weights of each larval sample are given in Table 54 together with the mean weights for freshly killed, newly emerged male and female adults which were similarly obtained during the spring. On each occasion at least 20 individuals were weighed.

Coulson (1962) and Hadley (1966) have presented growth curves for T.subnodicornis and M.ater respectively. Both show a rapid increase in larval weight from hatching to the onset of winter, but during the latter the increase in weight is small. In the spring increase in larval weight

again proceeds at a rapid rate. The data presented in Table 54 are confined to the last two instars of M.ater but demonstrate the slowing of growth during the winter.

TABLE 54. The mean wet weights (in mg) of M.ater larvae and adults

i) 1967

Date	Gley	Podsol	1700'	2050'	2500'	2700'
January	1.41	1.66				
February	1.58	1.61				
April	1.95	1.68	1.70	1.87	1.98	2.00
June ♀ Adults	0.77	0.65	0.66	0.90	0.84	0.82
June ♂ "	0.62	0.56	0.60	0.52	0.61	0.62

ii) 1968-69

Date	Gley	Podsol	Bl.Bog	1700'	1900'	2050'	2500'	2700'
October	0.89	0.92	0.76	0.71	0.69	0.97	0.63	
November	0.98	1.00	1.14	1.21	1.08	1.92	1.29	1.81
January				1.24	1.19	1.96		
April	1.93	1.78	1.89	1.87	1.76	2.20	1.77	2.05
June ♀ Adults	0.96	0.73	0.78	0.75	0.62	1.05	0.77	0.77
June ♂ "	0.65	0.55	0.62	0.63	0.54	0.64	0.57	0.63

In Table 55 the percentage increase in weight from November 1967 to April 1968 is presented together with the mean temperature for that period.

While the weight increases appear large at the relatively low mean temperatures, it must be remembered that these latter values, over the long time interval, may hide considerable upper excursions of temperature. The regression of increase in weight on temperature has the equation : $y = 23.1 + 37.0x$. However, with a standard deviation of 25.7 the data are so variable that the slope of the line is not significantly different from zero; $t = 1.851$ $df = 6$ $P > 0.10$.

TABLE 55. Increase in weight of larvae from November 1967 to April 1968 and mean temperature

Site	% increase in weight	Mean Temp. °C
1700'	54.5	1.40
1900'	63.0	0.99
2050'	14.6	0.83
2500'	37.2	0.33
2700'	13.3	-0.05
Gley	96.9	0.92
Podsol	78.0	1.34
Bl.Bog	65.8	0.76

Figure 24 illustrates the relationship between the mean weight of the fourth instar larvae in April and the mean weights of newly emerged male and female adults that they subsequently produce. In each case the sites with larvae of higher mean weight produce adults whose mean weights are also higher. The equations of the two lines are :

Larval weight and females : $y = -0.42 + 0.64\ x$

Larval weight and males : $y = 0.25 + 0.18\ x$

In each case the slope of the line is significantly different from zero : females, $t = 4.341$ df $= 12$ $P < 0.001$; males, $t = 2.901$ $df = 12$ $P < 0.02$. However, the slope of the regression of female weight against larval weight is significantly higher than that of male weight against larval weight; $t = 2.860$ $df = 14$ $P < 0.02$. It appears from here that any increase in mean weight of the larvae, contributes mainly to producing females of greater weight, while male adults are increased in weight by a factor that is 3.5 times smaller than the increase in female weight.

Figure 24. The relationship between the mean wet weights of the fourth instar larvae of M.ater in April, and the mean wet weights of the newly emerged male and female adults. that they subsequently produce. The equations of the two lines are :

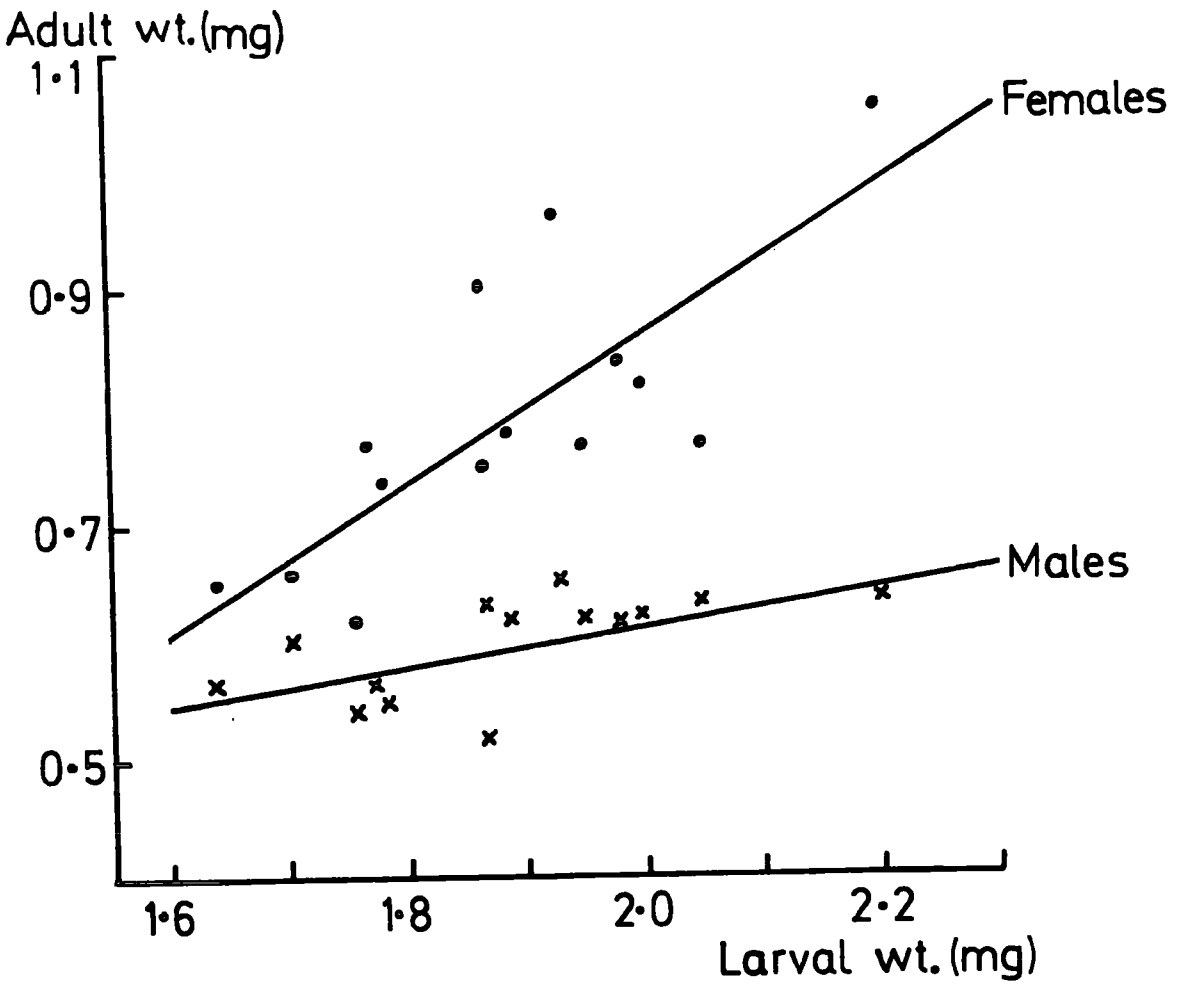
larval wt. and female wt. $y = -0.42 + 0.64 x$

larval wt. and male wt. $y = 0.25 + 0.18 x$

In each case the slope of the line is significantly different from zero :

females, $t = 4.341$ $df = 12$ $P < 0.001$

males, $t = 2.901$ $df = 12$ $P < 0.02$


Adult wt.(mg)
1·1
0·9
0·7
0·5
Females
Males
1·6
1·8
2·0
2·2
Larval wt.(mg)

A possible explanation for this is that, as the males have an excess of gametes even at the lower weights, there is little advantage in them increasing their weight. Increased weight might permit a greater amount of fat to be stored, and so prolong the adult life span, but with the excess of males in the population this is a small advantage compared to the increased weight of the females, which it will be shown below means that they contain more eggs when newly emerged. It is therefore reasonable to suggest that any increase of weight that is available to the population would be channelled into the female proportion which can utilise the food to produce more eggs.

Fecundity

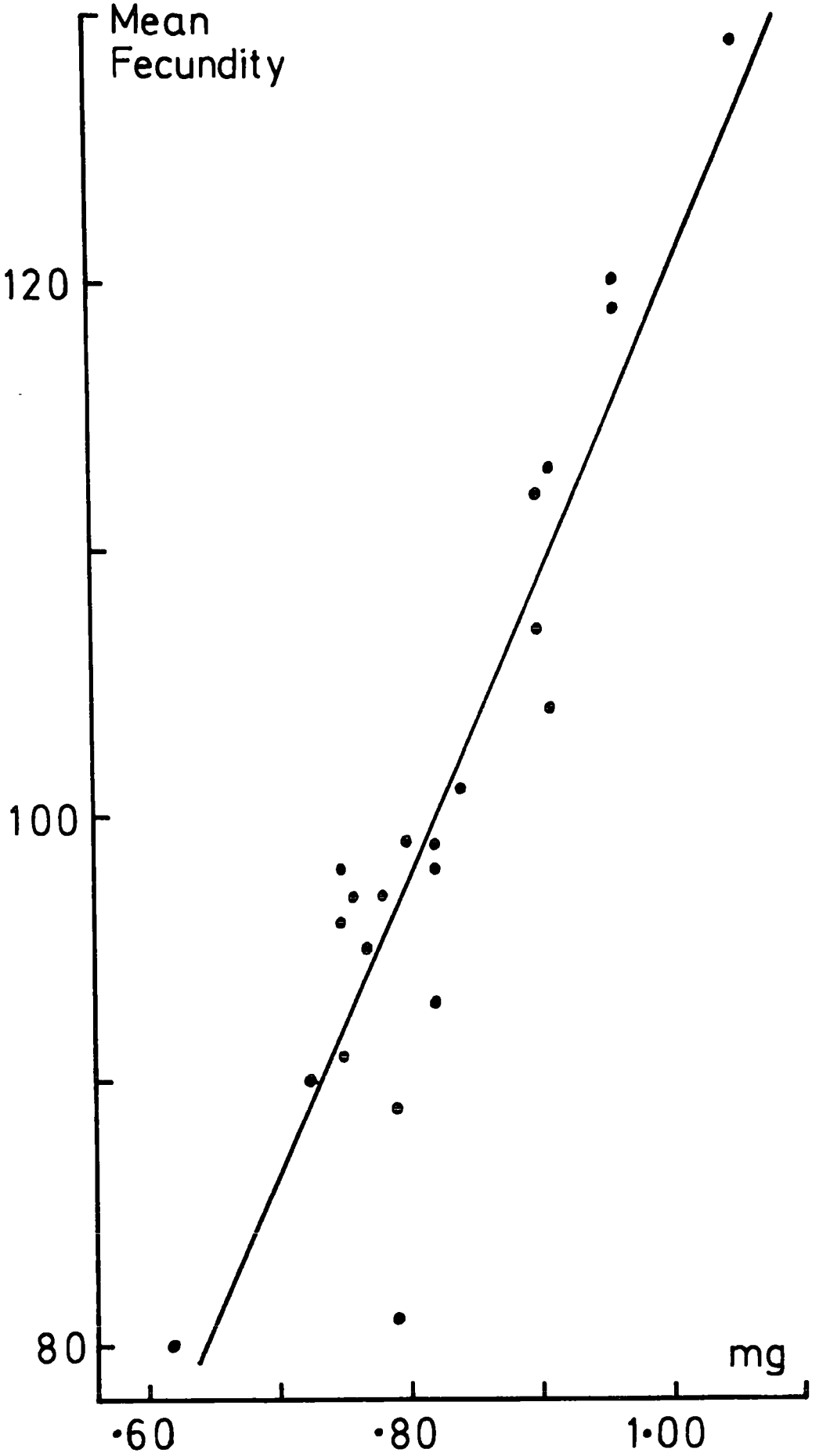
After samples of newly emerged females had been weighed they were dissected to determine the number of eggs they contained. Each mean fecundity presented in Table 56 was obtained by dissecting twenty to thirty newly emerged females. The results are illustrated in Figure 25 which shows the clear tendency for fecundity to increase with female weight. The correlation coefficient is +0.914 and the equation of the line is : $y = 4.58 + 116.13\,x$. The slope is significantly different from zero; $t = 10.35$ $df = 21$ $P < 0.001$.

TABLE 56. The mean wet weights of newly emerged females and their fecundity

Year	Site	Mean weight (mg)	Mean fecundity
1968	1700'	0.75	91
	1900'	0.62	80
	2050'	1.05	129
	2700'	0.77	95
	Gley	0.96	120
	Podsol	0.73	90
	Bl.Bog	0.78	97
1969	1400'	0.91	104
	1700'	0.84	101
	1900'	0.75	98
	2050'	0.80	99
	2700'	0.79	89
	Gley	0.90	107
	Podsol	0.81	93
	Bl.Bog	0.76	97
1970	1400'	0.90	112
	1700'	0.82	98
	1900'	0.75	96
	2050'	0.82	99
	2700'	0.91	113
	Gley	0.96	119
	Podsol	0.79	81

A similar relationship was found to exist between pupal weight and egg number by Hadley (1966) in his laboratory study, and he was also able to relate increase in pupal weight to an increase in the weight of the preceding instar four larvae. The mean weight data presented here also illustrate the tendency for increased spring instar four weights to produce heavier females and therefore more eggs.

Figure 25. The relationship between the mean fecundity and the mean wet weight of newly emerged M.ater females. The equation of the line is $y = 4.58 + 116.13x$ and the correlation coefficient, $r = +0.914$. The slope of the line is significantly different from zero : $t = 10.35$ $df = 21$ $P < 0.001$.

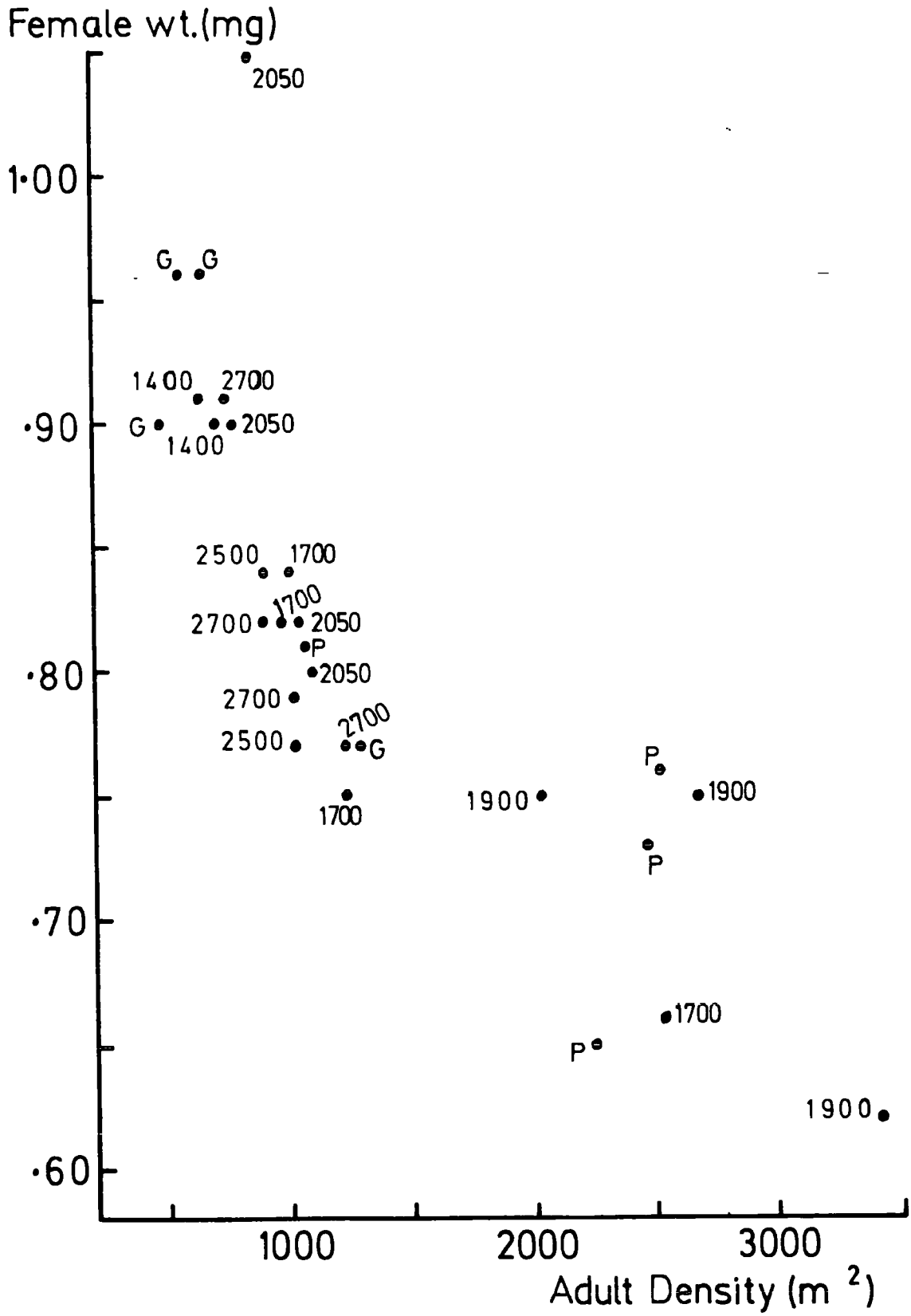

Mean
Fecundity
120
100
80
mg
·60
·80
1·00

5.6 Weight and Density of Adults

Comparison of the density of M.ater adults and the mean weight of newly emerged females indicates an inverse relationship between the two parameters. This is illustrated in Figure 26 which shows, with one exception, the 2050' in 1968, the closeness of the inverse relationship over the adult density range 500 - 1400 per sq.m. However, it is clear that the relationship is considerably more variable where adult density is above 2000 per sq.m. It is tempting to assume that the three lower points in this range, namely Podsol 1967, 1700' 1967, and 1900' 1968, represent the true sequence, as these agree well with a hyperbolic relationship between density and mean female weight. This, however, involves ignoring the remaining four points in this range, for whose position no explanation can be offered, so that in the absence of data for adult densities in the range 1400' - 2000 per sq.m, this is not a valid course of action.

One implication of the relationship up to 1400 per sq.m is that food could be acting as a limiting factor, such that the females are smaller at higher densities. However, as the adults do not feed, this relation should be found in the larvae, since larval weight has been shown to be closely related to female adult weight. The suggestion of food as a limiting factor begs the question of what precisely constitutes the food of the larvae. No observations on feeding have been made in the present study and Hadley was unable to provide much

Figure 26. The relationship between the density of M.ater adults and the mean wet weight of the newly emerged females.


Female wt.(mg)
1·00
·90
·80
·70
·60
2050
G
G
1400
2700
G
2050
1400
2500
1700
1700
2700
2050
P
2050
2700
2700
2500
G
1700
1900
1900
P
P
1700
P
1900
1000
2000
3000
Adult Density (m 2)

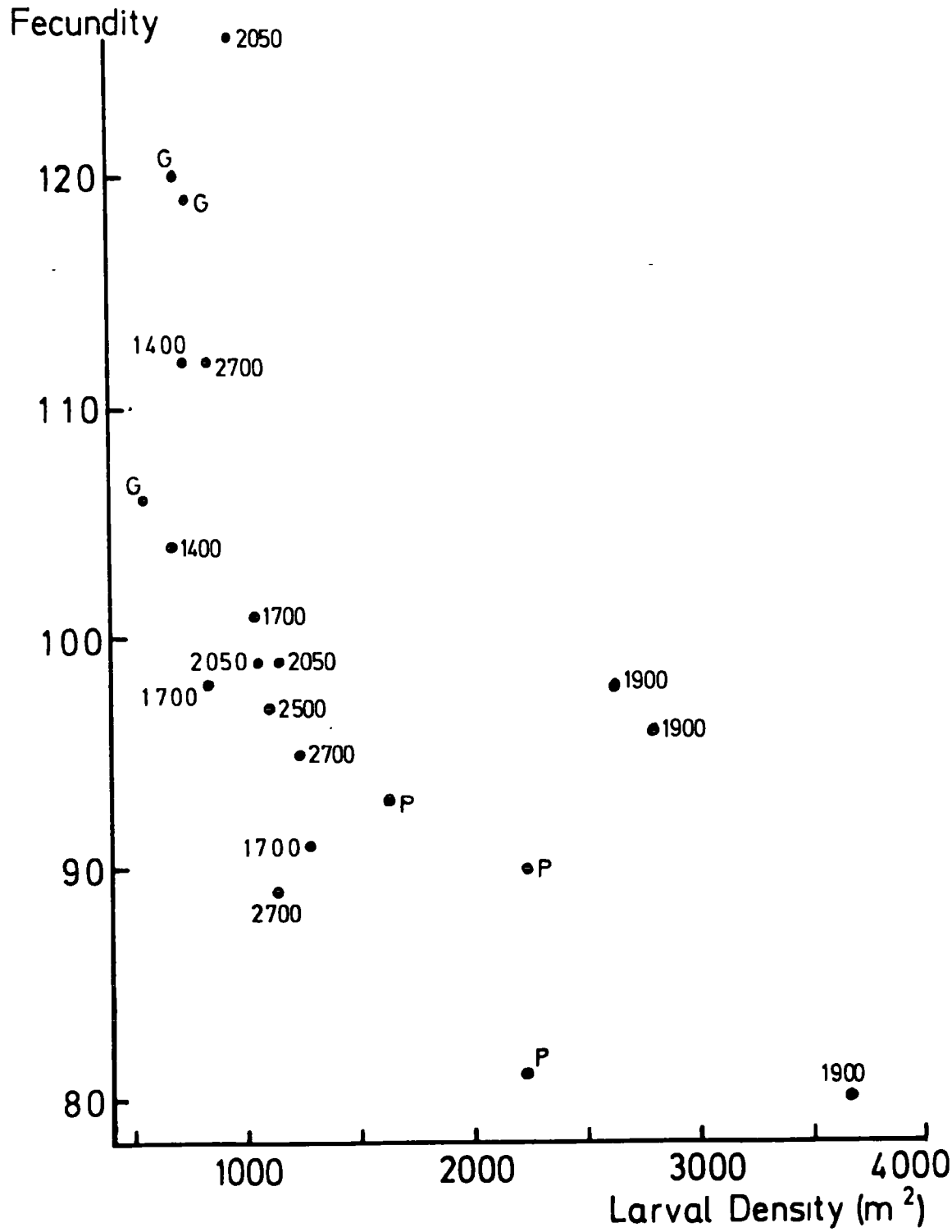
information on this topic other than that the food comprised partially decomposed detritus. He thought it unlikely that larvae fed directly on plant tissues, and the larvae failed to survive on cultures of isolated strains of moorland bacteria, algae, and fungi.

The distribution of the points in Figure 26 changes little if the density of spring larvae is placed on the horizontal axis in place of the density of the adults. This is to be expected since the population data presented later in this section show that a fairly constant mortality of about 5% occurs during pupation and emergence.

It has already been shown that adult female weight is closely related to the weight of spring larvae, but that male weight varies little with change in larval weight. It is therefore not surprising that when larval density is plotted against male weight, the relationship is much less clear.

The mean weight of adult females has been shown to be closely related to their mean fecundity. This is perhaps the most important implication of the density relationship, which is illustrated in Figure 27 where the mean fecundity is plotted against larval density. Thus, Figure 27 indicates a density dependent reduction in fecundity, though the variation in fecundity for any given larval density is often high. This is not surprising as data from several different sites are involved and there is no reason to assume that food

Figure 27. The relationship between the density of M.ater instar four larvae in the spring and the mean fecundity of the newly emerged females.


Fecundity
120
110
100
90
80
1000
2000
3000
4000
Larval Density (m 2)
2050
G
G
1400
2700
G
1400
1700
2050
2050
1700
2500
2700
P
1700
P
2700
P
1900
1900
1900

availability, if this is the cause, is identical at each site. Indeed, the one site, Blanket Bog, which does not agree with the general relationship, is the one site which is very different from the rest. If a series of Blanket Bog sites of different density were studied it is suggested that these would produce a general pattern similar to that presented in Figure 27.

When individual sites are considered in Figure the relationship between density and fecundity in general follows the overall trend indicating that the latter is not a chance occurrence through the combination of several sets of data.

A similar situation was found by Klomp (1966) in his study on the Pine Looper but he attributed the reduction in fecundity to growth inhibiting contact between larvae, an observation that was corroborated by Klomp & Gruys (1965) and Gruys (1970). Such inhibition is unlikely in M.ater though it deserves further investigation. The significance of the reduced fecundity as a regulatory factor is discussed later in this section where key factor and other analyses of population changes will be presented.

It is obviously important, in this context, that the density estimates are expressed on the basis of a unit that is comparable at all the different sites, and opinion has been divided on whether numbers per unit area, or per unit volume, should be used. For soil animals the suggestion of Weis-Fogh (1948) that the density should be expressed on the basis of the surface area of the soil pore

spaces available to each animal is ideal but not practicable. Macfadyen (1952) has discussed this topic and is in favour of densities expressed on a unit area basis for two main reasons. Firstly, the incident radiation from the sun that is the basis for all productivity studies is measured in terms of calories per unit area, and subsequent productivity studies use unit area as their basis. Secondly, and more relevant to the present study, the population density of the microflora and fauna is greatest at or just under the interface of the soil and the litter and the population density falls rapidly in either direction. This restriction in the vertical distribution of the soil fauna could lead to the relative overestimation of density on a unit volume basis where the litter was thinner.

While there is no clear boundary between the litter and soil surface at the Juncus squarrosus sites used in the present study, inspection of soil cores has failed to show any marked differences in the proportion of litter present at the different sites. Hadley (1966) found that approximately 73.0% of the larvae of M.ater occupied the top 3cm stratum, the base of which coincided with what may be taken as the interface between the soil and the litter. The use of a unit area basis seems quite adequate for the density estimates at these sites.

The Blanket Bog site, which had a distinct litter zone of about 4cm deep, was much more heterogeneous than the J.squarrosus sites, being dominated about equally by Calluna, Eriophorum, and Sphagnum. It may be that the

low densities recorded at this site are misleading because, for example, the larvae may be confined to the Calluna and Eriophorum litter and absent from the Sphagnum. The micro-distribution of the larvae within the Blanket Bog complex is a topic worthy of investigation, but in the absence of this an overall unit area basis has been used for comparison with the other sites and with the results of other workers at Moor House.

5.7 Analysis of changes in population density

Introduction

Of the nine sites from which information has been collected during this study, fairly complete records of the changes in population density of M.ater over a three year period are available for the majority. However, the Gley and Podsol sites were investigated by Hadley during 1964-66 and the use of his data, together with that collected by the present writer, has enabled life tables extending over six generations to be constructed.

The construction of life tables (Deevey 1947) is considered by Southwood (1966) to be vital to the description and understanding of the population dynamics of a species. The columns of the age specific life tables, all of which are presented in the appendix, are indicated by the usual symbols : l, d, and 100q, respectively representing the density in numbers per sq.m, the mortality in numbers per sq.m, and the percentage mortality. The methods by which the densities were measured have been described earlier in this section.

It has not been possible to make any direct measurements of mortality, and the values in the d column have all been obtained by subtracting successive density estimates.

5.7.1 The Peaty Podsol Site

It is recognised that in the life table any developmental stage does not have a monopoly of any given month, but the stage indicated represents the majority present at that time. It has been shown earlier in this section that fecundity fluctuates from year to year and, furthermore, that it has a relation to larval density. Reduction in fecundity is expressed in the life table by calculating the number of females of maximum mean fecundity, which at the Posdol site during 1965-70 was 93, that would be required to produce the same number of eggs into the next generation, a practice also adopted by Klomp (1966). Thus :

$$\text{Density of } ♀ \ (93) = \frac{\text{No.eggs laid}}{93}$$

The sex ratio is also considered as a similar mortality factor.

As Varley & Gradwell (1965) have shown, the stage selected as the basis for each generation may influence which factors appear to be most important in producing or regulating density fluctuations. In the present study the egg stage has been taken as the basis for each generation, an approach supported by Klomp (1966) in his study on the Pine Looper.

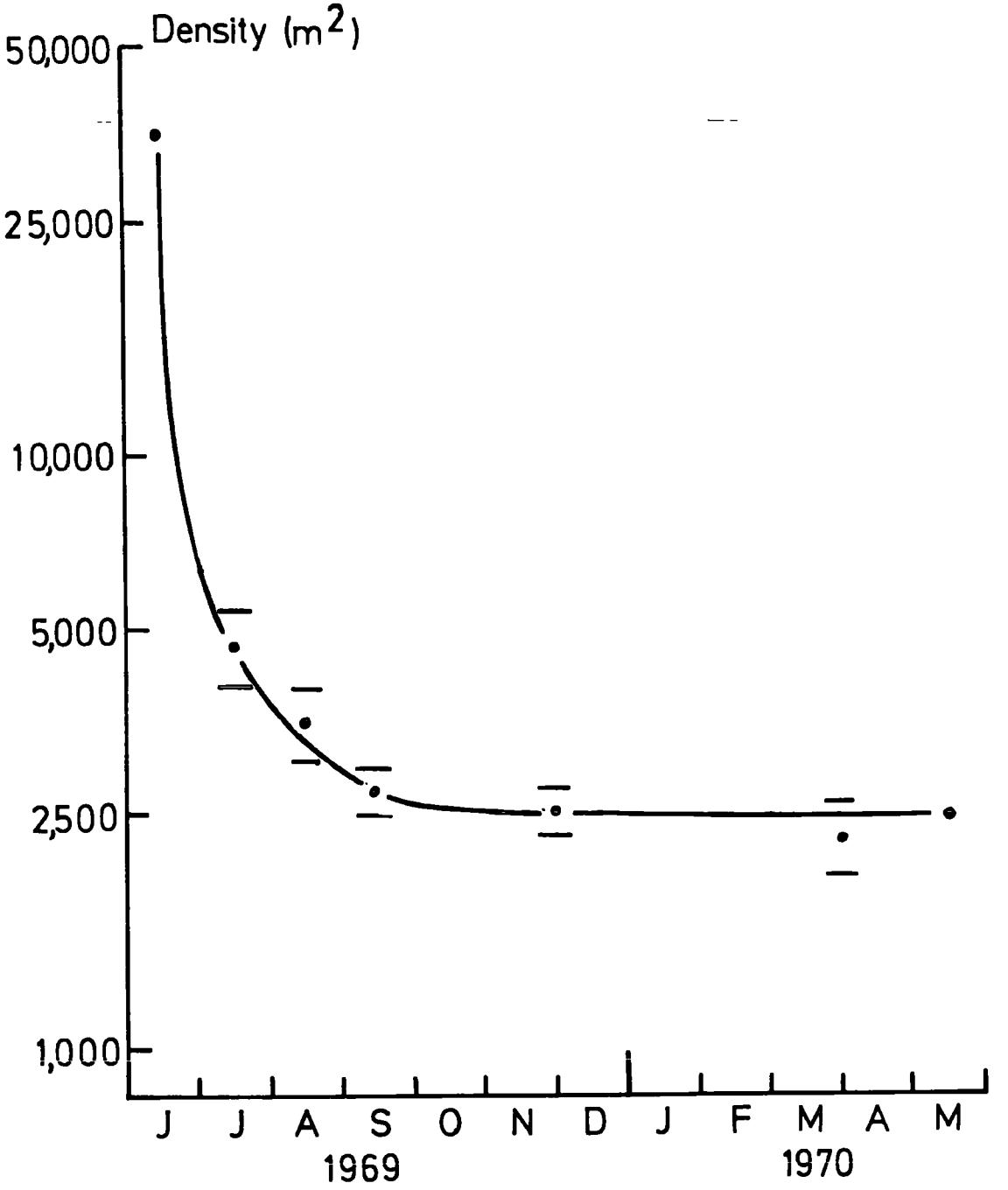
The Survivorship Curve

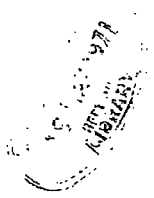
The fall in density with time is one of the simplest descriptions of life table data, and the survivorship curve for the Podsol site during 1969-70 is presented in Figure 28 as being generally typical of M.ater. It resembles type IV of Slobodkin (1962) in which mortality acts most heavily on the young stages so that within the first two months of the life cycle 90% of the total mortality has occurred. During August and September the mortality rate is more or less constant, after which there is relatively little reduction in numbers during the winter or during the spring emergence period. This pattern is similar to that recorded by Coulson (1962) for T.subnodicornis at Moor House, but he recorded an overwinter mortality of 40-50% compared with 12.2% for M.ater in 1969-70.

Key Factor Analysis

To obtain more precise information on which factors are largely responsible for changes in population density, and the way in which they act, some formalised and objective methods of inspecting life table data are clearly required. Morris (1963a, 1963b) introduced the method of key factor analysis in which the life table data are converted to logarithms, thus stabilising the variance and providing linearity for the regression of the log population of a chosen stage of generation n + 1, on the log population of generation n. Morris noted that the regression coefficient (b) described the extent to which

Figure 28. The survivorship curve for M.ater at the Peaty Podsol site 1969-1970. The horizontal lines indicate one standard error above and below the mean value.


Density (m^2)
50,000
25,000
10,000
5,000
2,500
1,000
J J A S O N D J F M A M
1969
1970



the rate of population increase fell off with increase in density. A coefficient of 1.0 implies no density dependence in the population, while very low values of b indicate a very high level of density dependence. Solomon (1964) has considered this relationship in greater detail and noted that a regression coefficient greater than unity indicates an inverse density dependent relationship. He also showed that the method can be used to assess the degree of density dependence in populations that are fluctuating mainly under the influence of density independent factors, but that phases of increase and decrease in the population density tend to require separate treatment.

The population data from the Podsol life tables are presented in Table 57 in logarithmic form, together with the age interval mortalities which will be referred to later. The fluctuations in density of the maximum fecundity females (females (93)) are illustrated in Figure 29 . The only excessive fluctuation in density was during 1969 where the value was relatively low. The relationship between generation n + 1 and generation n that has been discussed above is illustrated in Figure 30. where again the densities of females (93) are considered. The five points that are available clearly fall into two groups; those belonging to the ascending phase in Figure 29, namely, 1965-66, 1967-68, and 1969-70, and those belonging to the descending phase, namely, 1966-67, and 1968-69. The regression equation for the ascending

Figure 29. The fluctuations in the density, expressed as a logarithm, of the maximum fecundity females at the Peaty Podsol site 1965 - 1970.

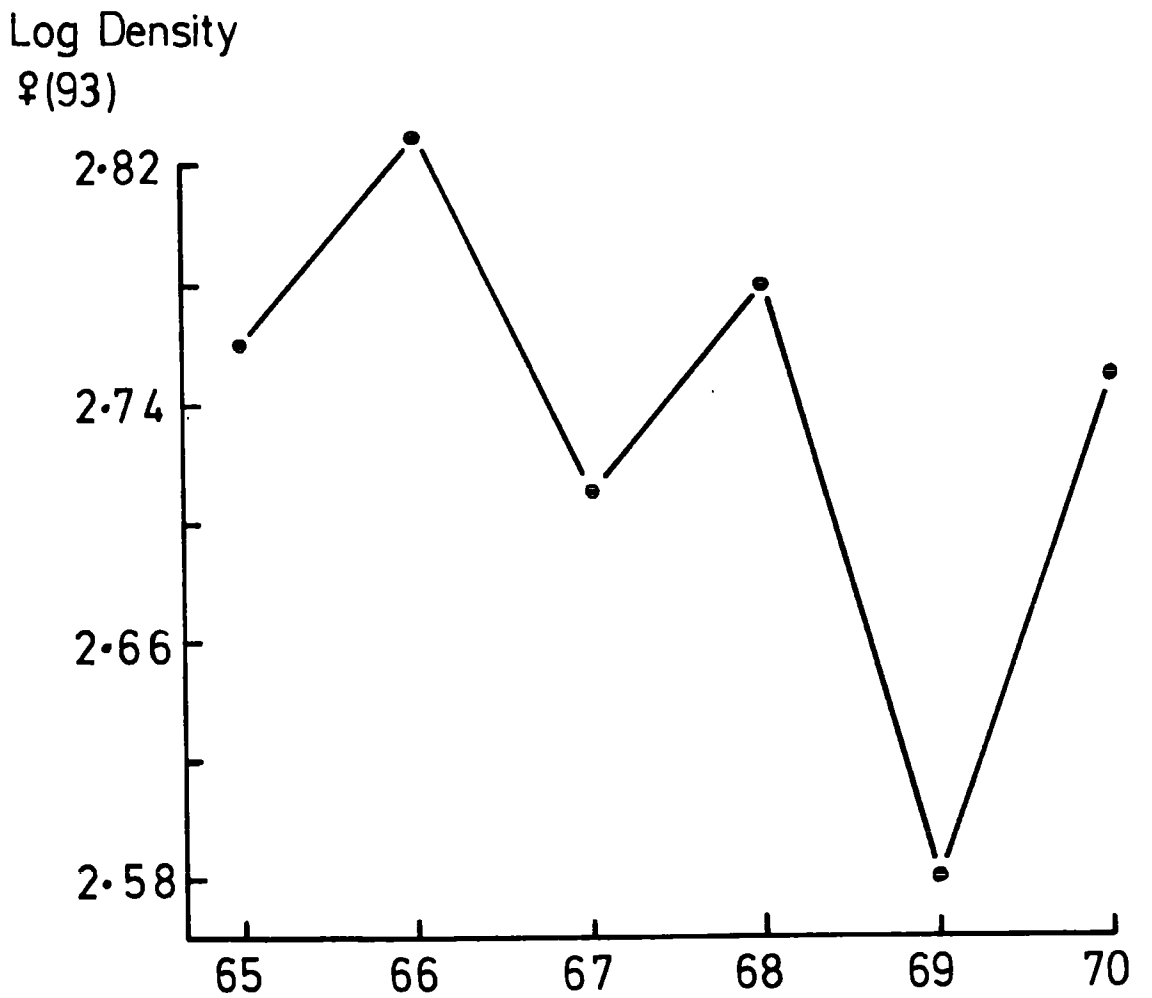
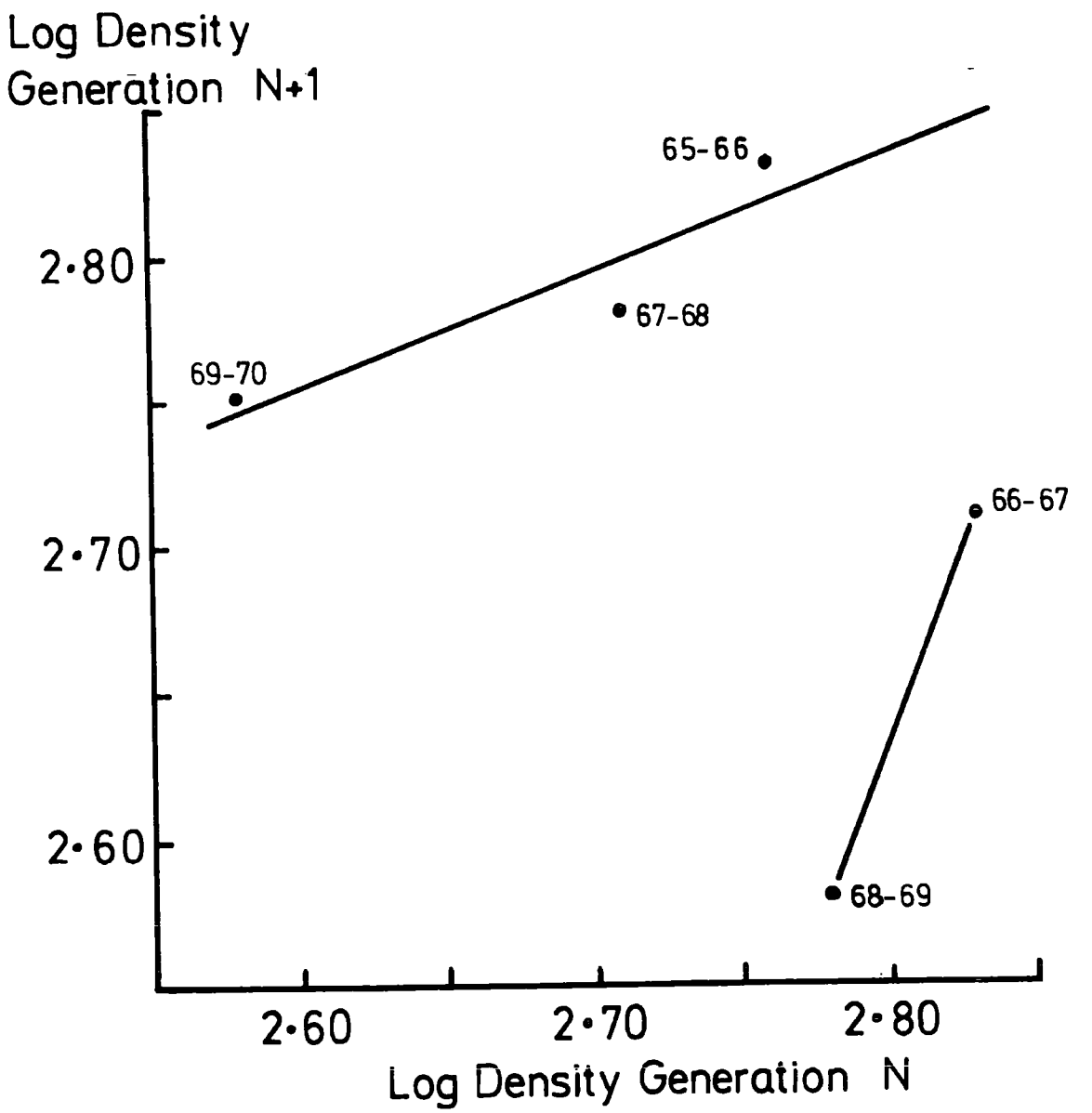

Log Density
♀(93)
2·82
2·74
2·66
2·58
65
66
67
68
69
70

Figure 30. The relationship between the log density of maximum fecundity females of M.ater in generation n and in generation n+1, at the Peaty Podsol site, 1965 - 1970. The regression equation for the ascending phase of the population is $y = 1.709 + 0.402x$ and the slope is significantly different from unity, $t = 3.572$ $df = 1$ $P < 0.05$. The slope for the descending phase is 2.600.


Log Density
Generation N+1
2·80
2·70
2·60
65-66
67-68
69-70
66-67
68-69
2·60
2·70
2·80
Log Density Generation N

phase is : $y = 1.709 + 0.402x$, the slope of which is significantly different from unity ($t = 3.572$, $P < 0.05$) and whose value of 0.402 is considered by both Morris and Solomon to indicate density dependent regulation. The slope for the descending phase is 2.600 which would indicate an inverse density dependent relationship, but with only two points,and with the particularly low density noted for 1969 this result is thought not to have any particular meaning.

Morris' method then requires the selection from biological knowledge of factors which might be important in producing population fluctuations and their correlation, each in turn with the generation mortality. Morris (1959) put forward the idea that, although many variables contributed to mortality in a population, the main fluctuations are due only to a few so called 'key factors'. A key factor is simply one that accounts for the main fluctuations in population size, and is not necessarily the principal regulatory or density dependent factor or factors (Varley & Gradwell 1960, Watt 1963). In general one would not expect the same factor to be both key and regulatory (Varley 1963) as the two are to some extent opposites. This distinction is emphasised by Solomon (1964).

The methods developed by Varley & Gradwell (1960, 1963, 1965) rely more heavily on graphical correlation and, in considering the whole generation, can show clearly in which age interval the density dependent and key factors lie. Klomp (1966) in his study of the

TABLE 57. Podsol population data as logarithms and age interval mortalities (k)

Stage	Time	1964-65 Log density	1964-65 k	1965-66 Log density	1965-66 k	1966-67 Log density	1966-67 k
Eggs	June	4.71		4.73		4.80	
	k_1		1.17		1.12		1.15
Inst.1	July	3.53		3.61		3.65	
	k_2		0.09		0.08		0.11
Inst.2	August	3.45		3.53		3.54	
	k_3		0.11		0.11		0.10
Inst.3	September	3.34		3.42		3.44	
	k_4		0.04		0.01		0.02
Inst.4	Nov-Dec	3.30		3.41		3.42	
	k_5		0.02		0.04		0.05
Inst.4	Mar-April	3.28		3.37		3.37	
	k_6		0.01		0.03		0.02
Adults	May-June	3.27		3.34		3.35	
	k_7		0.43		0.43		0.59
Adult ♀♀	May-June	2.84		2.91		2.76	
	k_8		0.08		0.08		0.05
♀♀ (93)	May-June	2.76		2.83		2.71	
GENERATION MORTALITY (K)			1.95		1.90		2.09

TABLE 57 (Contd.)

Stage	Time	1967-68 Log density	1967-68 k	1968-69 Log density	1968-69 k	1969-70 Log density	1969-70 k
Eggs	June	4.67		4.74		4.55	
k_1			0.88		1.10		0.89
Inst.1	July	3.79		3.64		3.66	
k_2			0.22		0.19		0.11
Inst.2	August	3.57		3.45		3.55	
k_3			0.14		0.18		0.12
Inst.3	September	3.43		3.27		3.43	
k_4			0.05		0.00		0.03
Inst.4	Nov-Dec	3.38		3.27		3.40	
k_5			0.03		0.06		0.05
Inst.4	Mar-April	3.35		3.21		3.35	
k_6			0.00		0.18		0.00
Adults	May-June	3.40		3.03		3.40	
k_7			0.56		0.45		0.54
Adult ♀♀	May-June	2.79		2.58		2.81	
k_8			0.01		0.00		0.06
♀♀ (93)	May-June	2.78		2.58		2.75	
GENERATION MORTALITY (K)			1.89		2.16		1.80

population dynamics of the Pine Looper has used a combination of Varley & Gradwell's method and Morris' method.

The comparison of age interval mortalities with fluctuations in generation mortality is presented in Figure 31 for the Podsol site, following the method of Varley and Gradwell. The age interval mortalities k_{1-8} are not necessarily strictly mortalities but rather represent the loss of larvae or adults from the population because they are all derived from the difference of

successive population estimates. The mortality ascribed to each k value represents the largest mortality thought to be occurring over that period, though it is appreciated that other factors may also be operating.

Egg mortality, k_1, and first instar mortality, k_2, have been combined in Figure 31 because even slightly different times of sampling the first instar population in each year produce widely uncomparable results when natality and mortality are proceeding at a rapid rate. Further, the egg mortality, k_1, includes a variety of separate factors, such as death of the females before all the eggs are laid, variations in fertility, and mortality proper, through physical effects, for instance, desiccation, and biological ones, for instance, predation. No direct evidence is available that would permit these factors to be separated.

It is clear from a visual inspection of Figure 31 that k_{1+2} is most clearly correlated with generation mortality K. However, in Table 58 the correlation coefficients for each k factor against K are presented, together with the probability level.

Only k_{1+2} shows a significant correlation and obviously represents the largest key factor; its coefficient of determination, $r^2 = 0.719$, indicating that 71.9% of the variation in generation mortality is accounted for by egg and first instar mortality. A secondary key factor is k_6, the pupation and emergence mortality whose coefficient of determination indicates that it alone would account for 57.3% of the variation in generation mortality.

Figure 31. A comparison of the age interval mortalities with the fluctuations in generation mortality of the M.ater population at the Peaty Podsol site 1964 - 1970.

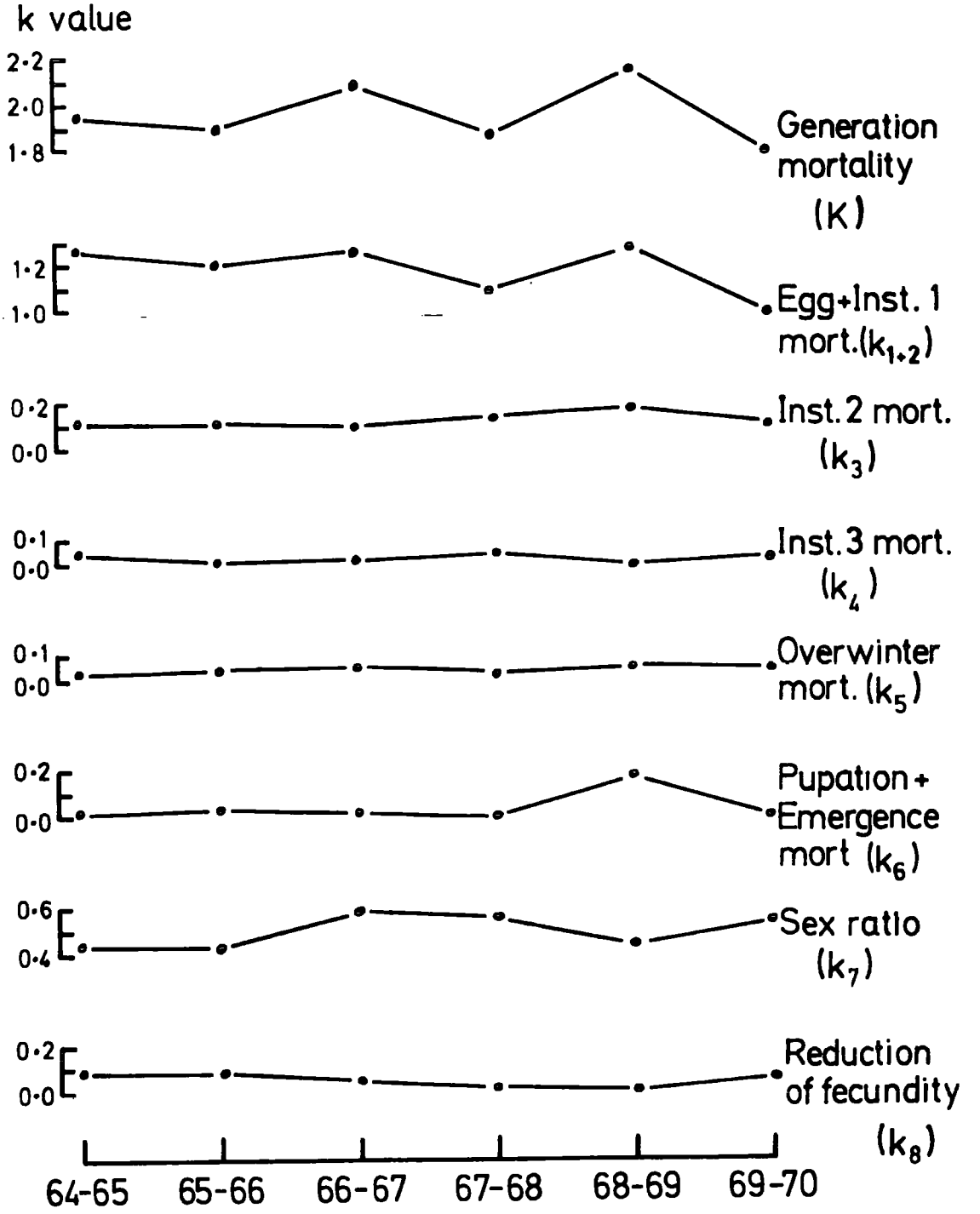

k value
2·2
2·0
1·8
Generation mortality (K)
1·2
1·0
Egg+Inst. 1 mort.(k_{1+2})
0·2
0·0
Inst. 2 mort. (k_3)
0·1
0·0
Inst. 3 mort. (k_4)
0·1
0·0
Overwinter mort. (k_5)
0·2
0·0
Pupation + Emergence mort (k_6)
0·6
0·4
Sex ratio (k_7)
0·2
0·0
Reduction of fecundity (k_8)
64-65
65-66
66-67
67-68
68-69
69-70

TABLE 58. The correlation between generation mortality (K) and each age specific mortality (k_1-k_8) at the Peaty Podsol site. In each case there are four degrees of freedom

Correlation of K with :	correlation coefficient	probability
k_{1+2}	0.848	< 0.05
k_3	0.428	> 0.10
k_4	-0.591	> 0.10
k_5	0.458	> 0.10
k_6	0.757	$< 0.10 > 0.05$
k_7	-0.081	> 0.10
k_8	-0.465	> 0.10

The various k factors have been tested for direct density dependence by plotting each against the number entering the stage on which it acts. In a direct density dependent situation k will increase as the numbers entering the relevant stage increase. In Table 59 the series of regression equations are given together with the standard deviation and the probability that the slope of the line is significantly different from zero.

The slopes of the regression lines are significantly different from zero on two occasions, which are illustrated in Figures 32 and 33. These are egg and first instar mortality and reduction in fecundity, and some density dependent effect can be suspected to be operating here. However, as the two variables are not independent, k being derived partly from the population density at the beginning of the stage on

which it acts, the regression could be spurious. Therefore in a consideration of k_{1+2} the regression of log egg density and log instar two density is carried out, and for k_8 the regression of log female density and log female (93) density. This is the same test for density dependent action between successive stages, as has been carried out earlier for density dependent action between successive generations. These regression equations are given in Table 60. Both Southwood (1966) and Varley & Gradwell (1963, 1968) have stated that because both stages may show an equal amount of sampling variation, both the regression of stage $_n$ on stage $_{n+1}$ and stage $_{n+1}$ on stage $_n$ must be performed, and that both regression coefficients must differ significantly from zero before density dependence is proved.

TABLE 59. The regression equations between mortality and density to detect density dependence at the Peaty Podsol site

Y axis	X axis	Regression equation	S.D. Y on X	Probability of the slope being sig. different from zero
k_{1+2}	log dens Eggs	$y = -4.46 + 1.20\ x$	0.055	< 0.02
k_3	" Inst 2	$y = 0.85 - 0.21\ x$	0.031	> 0.10
k_4	" Inst 3	$y = -0.37 + 0.12\ x$	0.019	> 0.10
k_5	" Inst 4 (autumn)	$y = 0.01 + 0.01\ x$	0.016	> 0.10
k_6	" Inst 4 (spring)	$y = 2.98 - 0.88\ x$	0.045	> 0.05
k_7	" Adults	$y = -0.42 + 0.28\ x$	0.067	> 0.10
k_8	" Adult ♀	$y = -0.66 + 0.25\ x$	0.022	< 0.05

Figure 32. The relationship between the M.ater egg and first instar mortality, k_{1+2}, and the log egg density at the Peaty Podsol site, 1965 - 1970. The equation of the line is $y = -4.455 + 1.20\,x$ and the slope is significantly different from zero : $t = 4.138$ $df = 4$ $P < 0.02$.

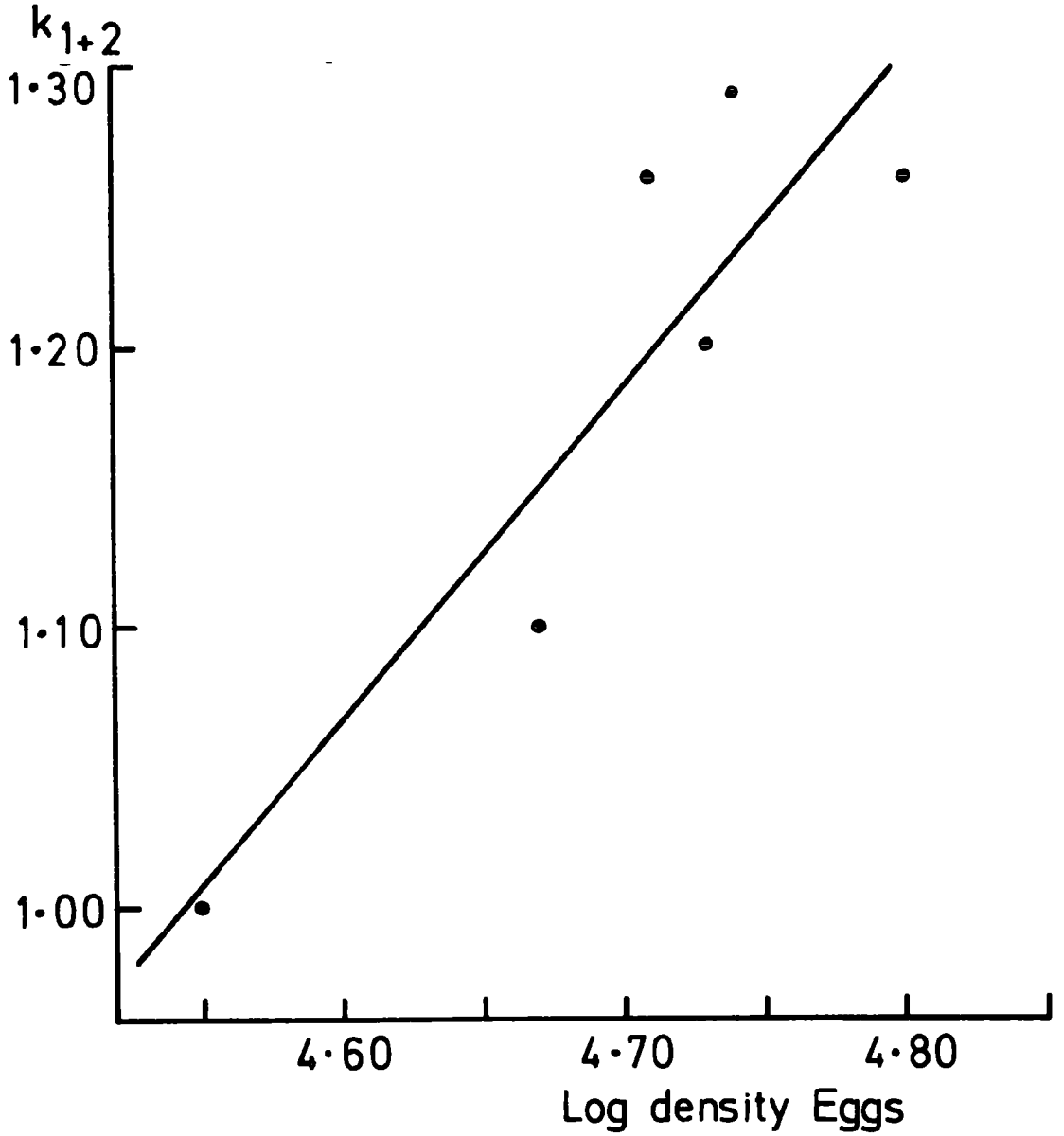

k1+2
1·30
1·20
1·10
1·00
4·60
4·70
4·80
Log density Eggs

Figure 33. The relationship between the reduction in fecundity, k_8, of M.ater and the log female density at the Peaty Podsol site, 1965 - 1970. The equation of the line is $y = -0.656 + 0.253\,x$ and the slope is significantly different from zero : $t = 2.822$ $df = 4$ $P < 0.05$.

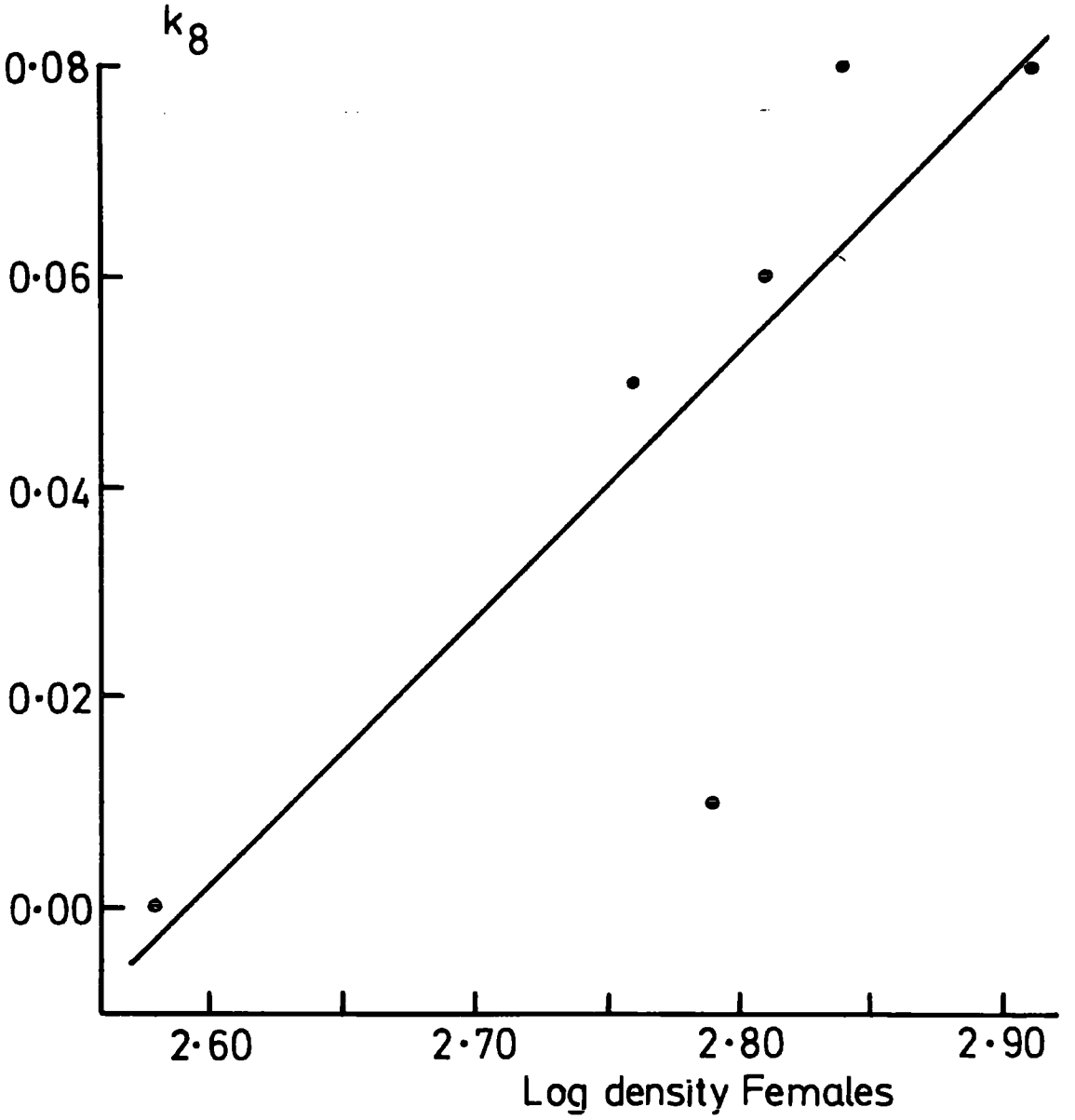

k_8
0·08
0·06
0·04
0·02
0·00
2·60
2·70
2·80
2·90
Log density Females

TABLE 60. The regression equations between successive stages in the population at the Peaty Podsol Site to demonstrate density dependent mortality, in k_{1+2} and k_8

Y axis	X axis	Regression equation of	S.D. Y on X	Prob.of slope being sig. diff. from unity
log density Instar 2	log density Egg	$y = 4.46 - 0.20\ x$	0.055	<0.05
log density Egg	log density Instar 2	$y = 6.57 - 0.53\ x$	0.090	>0.10
log density ♀ (93)	log density ♀	$y = 0.66 + 0.75\ x$	0.022	<0.05
log density ♀	log density ♀ (93)	$y = -0.67 + 1.27\ x$	0.029	>0.10

Table 60 indicates that density dependent action cannot be conclusively proved. When log density of instar two is regressed onto log density of eggs, the slope is significantly different from unity, but when the axes are reversed this is not so. Similarly, when log density of the maximum fecundity females is regressed on to log density of the females, the slope is significantly different from unity, but the reverse is not so. It is thought that this is largely an effect of the few points that are available and that density dependence may still be assumed to operate here. The negative slopes in the first pair of equations are not significantly different from zero and are thought to be of no consequence. Before further discussion of these findings the population data from the Peaty Gley Site will be considered.

5.7.2 The Peaty Gley Site

Life tables for the period 1964 to 1970 for the Peaty Gley site are presented in the appendix. The analysis of the population data from this site will be the same as the data from the Peaty Podsol site, and the data are presented in logarithmic form in Table 61.

The fluctuations in density of the maximum fecundity females (females (120)) are illustrated in Figure 34. This may be compared with Figure 29 which presents the same information for the Podsol site. The Gley site supports a population that is generally of lower density than that at the Podsol site, and the pattern of fluctuation at the Gley site might be the descending component of an oscillation cycle lasting six to seven years. The Podsol data could indicate a cycle of oscillation of around two years, but the data are very limited in this respect. However, the highest density of maximum fecundity females occurs in the same year, 1966, at both sites, as does the minimum density, in 1969. Whether this may be the result of some climatic factor will be discussed later.

Evidence of some density dependent regulation at the Gley site is shown in Figure 35 where log density of maximum fecundity females for generation n+1 is plotted against the same parameter for generation n. The regression coefficient for the descending phase is $b = 0.714$ which is larger than that for the Podsol site but nonetheless indicates the presence of some density

Figure 34. The fluctuations in the density, expressed as a logarithm, of the maximum fecundity females of M.ater at the Peaty Gley site, 1965 - 1970.

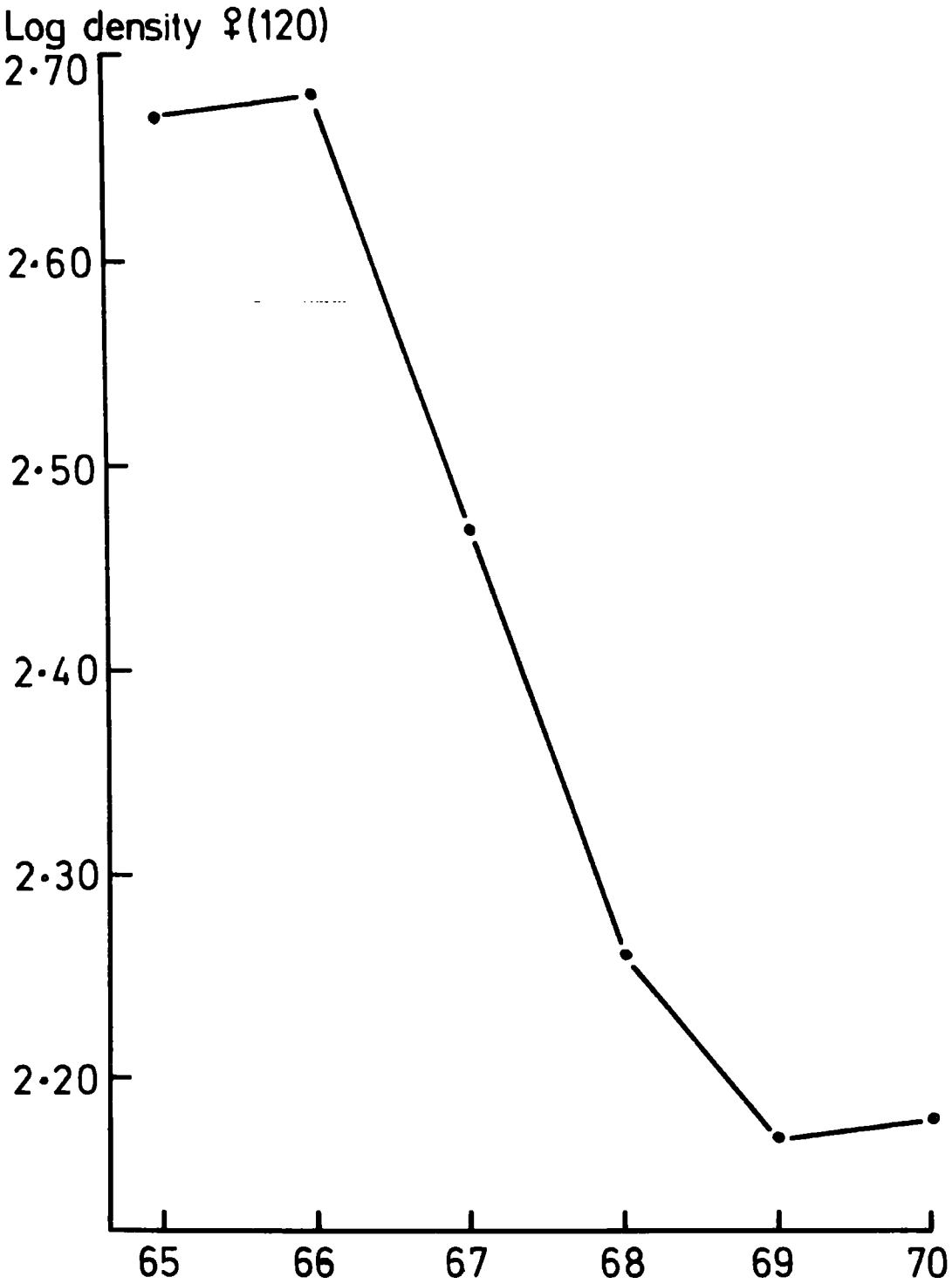
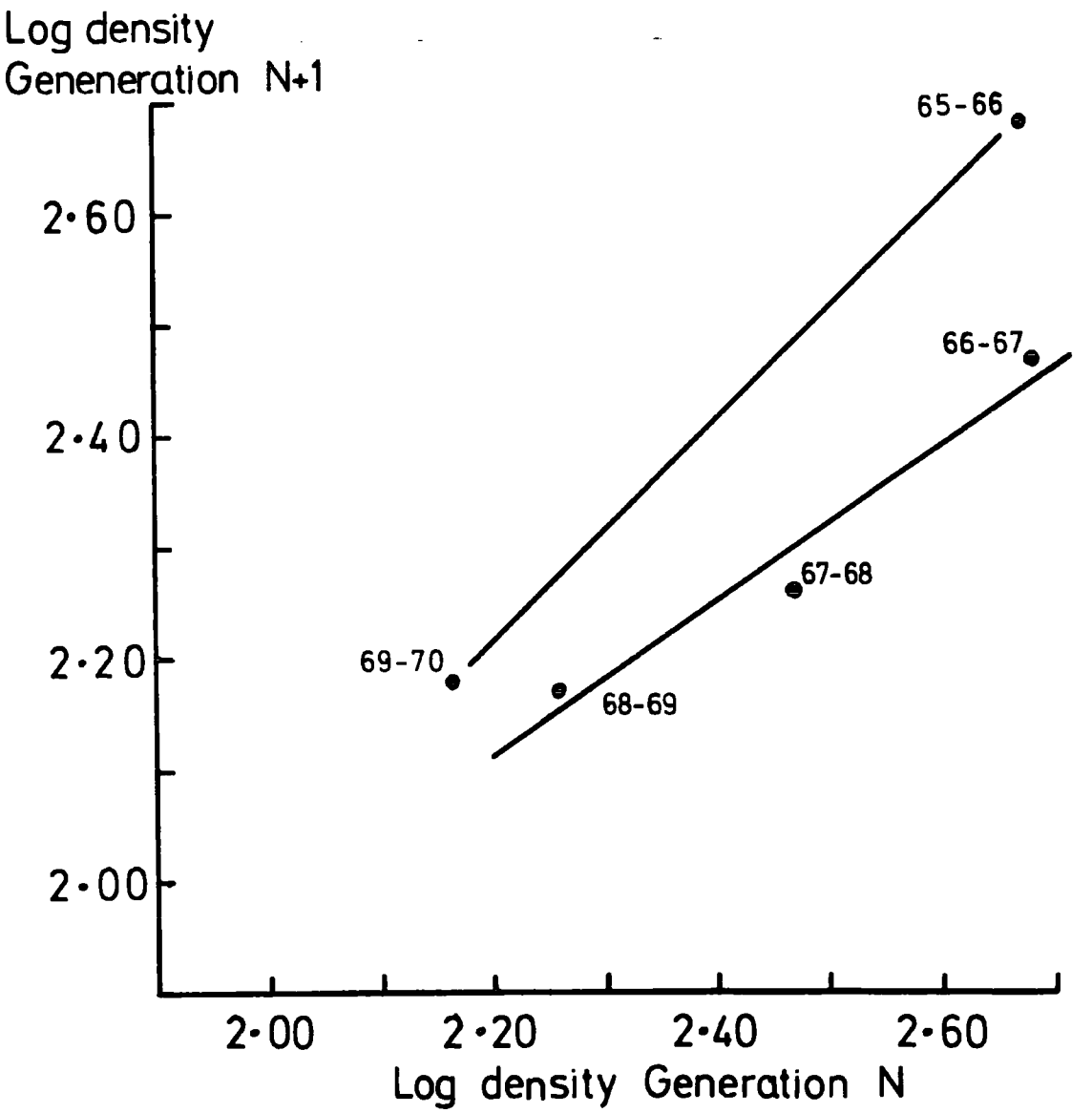

Log density ♀(120)
2·70
2·60
2·50
2·40
2·30
2·20
65
66
67
68
69
70

Figure 35. The relationship between the log density of the maximum fecundity females of M.ater in generation n and in generation n+1, at the Peaty Gley site 1965 - 1970. The regression equation for the descending phase of the population is, $y = 0.536 + 0.714\ x$. The slope of the ascending phase is 1.000.


Log density
Genenerating N+1
2·60
2·40
2·20
2·00
65-66
66-67
67-68
68-69
69-70
2·00
2·20
2·40
2·60
Log density Generation N

dependent regulation. The slope for the ascending phase is 1.00 which would indicate no regulation, but only two points are involved.

The graphical comparison of the age interval mortalities with the fluctuations in generation mortality is presented in Figure 36, and the table of correlation coefficients, Table 62, confirms that egg and first instar mortality represents the largest key factor. In Table 62 the correlations for both the Gley site and the Podsol site are presented for comparison.

The coefficient of determination, $r^2 = 0.469$, is lower for k_{1+2} at the Gley site, although this is compensated for by the subsequently higher k_3 correlation, but both sites are consistent in having egg and first instar mortality as the first key factor. While pupation and emergence mortality was a second key factor at the Podsol site, it has no significant action at the Gley site. The fluctuating sex ratio ranks as the second key factor at the Gley site, though its action is at a low level. The negative effect of reduction in fecundity at the Gley site may be noted here, and will be considered later in more detail in the context of density dependence.

TABLE 61. Gley population data as logarithms and age interval mortalities (k)

Stage	Time	1964-65 Log density	1964-65 k	1965-66 Log density	1965-66 k	1966-67 Log density	1966-67 k
Eggs	June	4.44		4.75		4.76	
k_1			0.93		1.11		1.11
Inst.1	July	3.51		3.64		3.65	
k_2			0.09		0.10		0.27
Inst.2	August	3.42		3.54		3.38	
k_3			0.03		0.07		0.19
Inst.3	Sept.	3.39		3.47		3.19	
k_4			0.06		0.02		0.04
Inst.4	Nov-Dec	3.33		3.45		3.15	
k_5			0.01		0.08		0.02
Inst.4	Mar-Apr	3.32		3.37		3.13	
k_6			0.03		0.05		0.03
Adults	May-June	3.29		3.32		3.10	
k_7			0.43		0.45		0.54
Adult ♀♀	May-June	2.86		2.87		2.56	
k_8			0.19		0.19		0.09
♀♀ (120)	May-June	2.67		2.68		2.47	
GENERATION MORTALITY (K)			1.77		2.07		2.29

TABLE 61 (contd.)

		1956-68		1968-69		1969-70	
Stage	Time	Log density	k	Log density	k	Log density	k
Eggs	June	4.55		4.34		4.25	
k_1			0.95		0.94		0.77
Inst.1	July	3.60		3.40		3.48	
k_2			0.29		0.21		0.15
Inst.2	August	3.31		3.19		3.33	
k_3			0.18		0.19		0.29
Inst.3	Sept	3.13		3.00		3.04	
k_4			0.11		0.00		0.04
Inst.4	Nov-Dec	3.02		3.04		3.00	
k_5			0.17		0.26		0.12
Inst.4	Mar-Apr	2.85		2.74		2.88	
k_6			0.04		0.07		0.05
Adults	May-June	2.81		2.67		2.83	
k_7			0.55		0.45		0.57
Adult ♀♀	May-June	2.26		2.22		2.26	
k_8			0.00		0.05		0.08
♀♀ (120)	May-June	2.26		2.17		2.18	
GENERATION MORTALITY (K)			2.29		2.17		2.07

If the overall summer mortality of both populations is considered it is clear that there is a high and consistent correlation of k_{1+2+3} against generation mortality K :

Podsol $r = 0.900$

Gley $r = 0.939$

Figure 36. The comparison of the age interval mortalities of M.ater with the fluctuations in generation mortality, at the Peaty Gley site, 1964 - 1970.

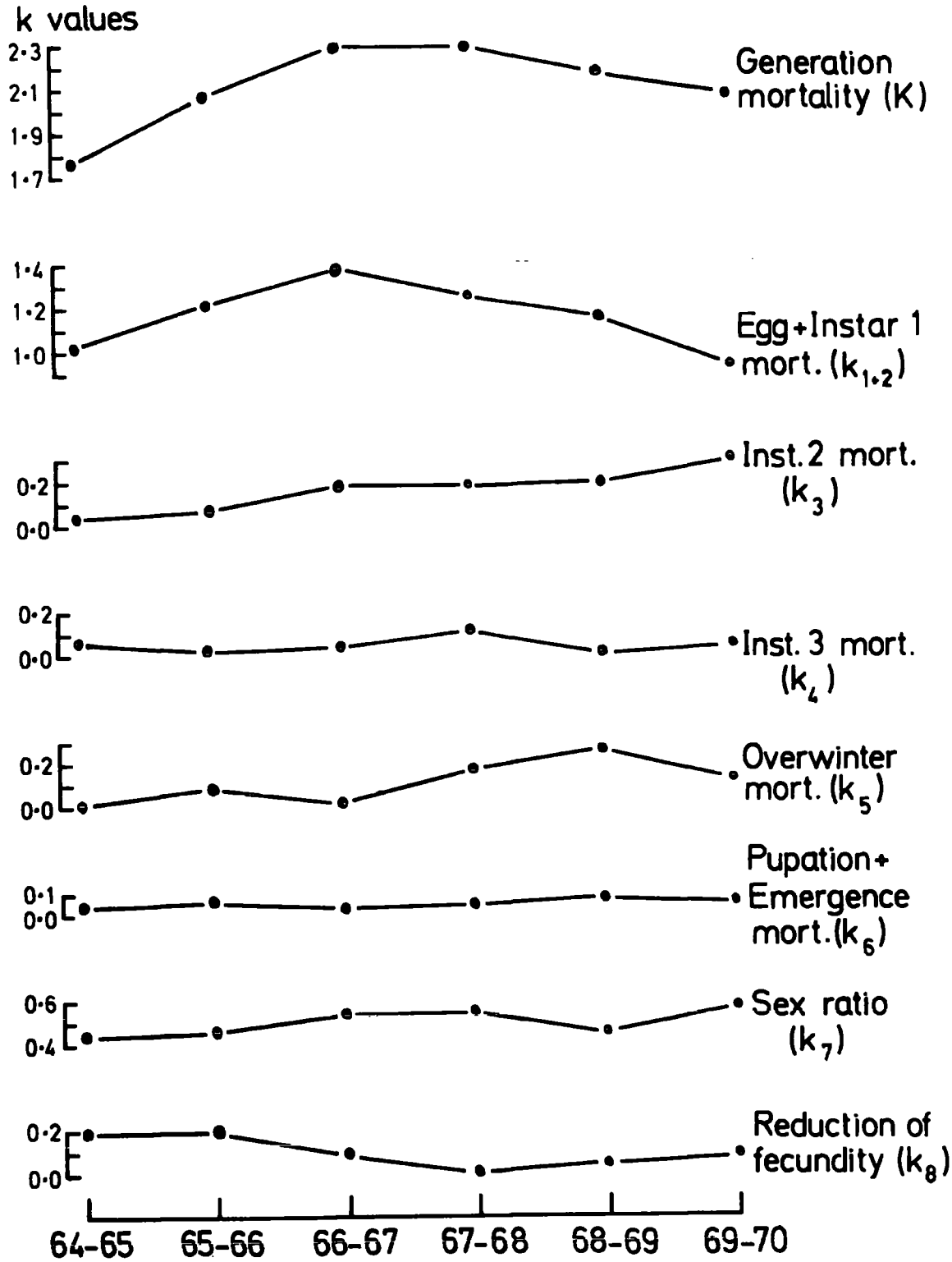

k values
2·3
2·1
1·9
1·7
Generation mortality (K)
1·4
1·2
1·0
Egg+Instar 1 mort. (k_{1+2})
0·2
0·0
Inst.2 mort. (k_3)
0·2
0·0
Inst. 3 mort. (k_4)
0·2
0·0
Overwinter mort. (k_5)
0·1
0·0
Pupation+ Emergence mort.(k_6)
0·6
0·4
Sex ratio (k_7)
0·2
0·0
Reduction of fecundity (k_8)
64-65
65-66
66-67
67-68
68-69
69-70

TABLE 62. The correlation between generation mortality (K) and each age specific mortality k_{1-8} for the Gley and Podsol sites

Correlation of K with :	Corr.Coeff.Gley	Corr.Coeff.Podsol
k_{1+2}	0.685	0.848
k_3	0.588	0.428
k_4	0.115	-0.591
k_5	0.417	0.458
k_6	0.177	0.757
k_7	0.609	-0.081
k_8	-0.760	-0.465

The coefficients of determination indicate that this combined egg, first instar, and second instar mortality can account for 81.0% and 88.2% of the variation in generation mortality at the Podsol and Gley site respectively. Of the other mortality factors, only k_5, overwinter mortality, shows a similar value at each site, but with r = 0.458 at the Podsol site and r = 0.417 at the Gley site, it cannot be considered as an important key factor.

To test for density dependent action in each of the mortality factors the regressions of each k factor against the numbers entering the stage on which it acts are given in Table 63.

The slopes of two of the regressions, those for egg and first instar mortality, and for reduction in fecundity, are significantly different from zero. The action of a density dependent factor is further indicated for k_{1+2} by the regression of log density of instar two on log density

TABLE 63. The regression equations between mortality and density to detect density dependent mortality at the Peaty Gley Site

Y axis	X axis	Regression equation	S.D. of Y on X	Probability of slope being sig.different from zero
k_{1+2}	log dens Egg	$y = -1.77 + 0.65\ x$	0.062	< 0.02
k_3	" Inst 2	$y = 1.79 - 0.49\ x$	0.084	> 0.10
k_4	" Inst 3	$y = 0.02 + 0.01\ x$	0.042	> 0.10
k_5	" Inst 4 (autumn)	$y = 1.08 - 0.31\ x$	0.085	> 0.10
k_6	" Inst 4 (spring)	$y = 0.14 - 0.03\ x$	0.014	> 0.10
k_7	" Adults	$y = 0.80 - 0.10\ x$	0.062	> 0.10
k_8	" Adult ♀	$y = 0.48 + 0.23\ x$	0.032	< 0.01

of eggs, where :

$$y = 1.77 + 0.35\ x$$

The slope of 0.35 is significantly different from unity, $t = 3.019$, $P < 0.05$. Similarly the density dependent action of k_8 can be shown by the regression of log density of females (120) on log density of females. The equation here is :

$$y = 0.48 + 0.77\ x$$

and the slope is again significantly different from unity, $t = 4.960$, $P < 0.01$. When the axes in each regression are reversed, the slopes are no longer significantly different from unity, but this has been assumed not to detract too much from the general conclusions of density dependent action.

5.7.3. Discussion

The foregoing analyses indicate that at both the Podsol and Gley sites egg and first instar mortality is acting as a key factor, and when this is combined with instar two mortality about 90% of the variation in generation mortality from year to year can be accounted for. At each site there are two density dependent factors operating; egg and first instar mortality, and reduction in fecundity.

Egg and First Instar Mortality

It has been stated earlier that it is unusual for the key factor to operate in a density dependent way, and it is likely that it is the different components in this group that are having different effects.

a) Eggs Unlaid

No direct information is available about the percentage of eggs that remain unlaid by the female. Hadley (1966) showed that within 24 hours of mating over 60% of M.ater females had laid all their eggs, while the remainder still contained about 10% of their estimated original number. Similar results were obtained by Coulson (1962) for Tipula subnodicornis. It is not thought that this factor has an important effect within the k_{1+2} mortality complex.

b) Eggs Not Hatching

During his study in 1954 and 1955 Coulson examined over one thousand eggs of T.subnodicornis that had been laid in the peat. His samples were taken after all hatching had been completed and he was able to separate three classes of eggs :

1. Those that had hatched normally 76%
2. Those that had not hatched 16%
3. Those with the chorion split or holed 8%

No information was available about the number of eggs that might have completely disappeared, and these estimates must be taken as minima. Coulson noted that the last category indicated the activity of predatory arthropods, and that the second was due to infertility or death during egg development. In considering the two years separately he found that there was no significant difference between the percentages present in his second category, but there was a marked difference between mortality due to predation in each year.

In a laboratory culture Barnes (1937) found that only 46% of the eggs laid by T.paludosa successfully developed into larvae, and Hadley (1966) who induced Mater females to deposit their eggs on agar plates in the laboratory found an egg mortality in excess of 80%. This latter value is probably higher than that in the field; Coulson (1956) recorded a 53% mortality for T.subnodicornis eggs in the laboratory, a result much higher than his field measurements.

It is clear that infertility and egg mortality due to factors other than predation or parasitism cannot easily be separated. Hadley's laboratory estimate of 80% mortality is unlikely to be due to infertility alone. The effect of a virus or bacterial infection cannot be ruled out, but

no evidence for it has been reported. Several authors have reported large mortalities in the egg and first instar stages of crane-flies, and they frequently related them to desiccation (Rennie, 1917, Rogers 1942, Coulson 1962, Milne, Coggins & Laughlin 1965). In the present study it is thought that desiccation plays an important part in egg mortality, but it cannot be separated from infertility. With what is little more than an inspired guess it is suggested that the average mortality of 93% for the egg and first instar stages is made up as follows :

Eggs not laid	4%
Infertility and desiccation	50%
Predation	39%
Total :	93%

Thus infertility and desiccation is thought to be acting as the key factor, and predation as the density dependent factor.

The lower value of egg mortality found by Coulson could be due to the tough chorion of T.subnodicornis eggs affording more protection from desiccation, and the ability of the larger fly to lay eggs deeper below the ground surface. However, Coulson did find a high mortality in the first two instars of T.subnodicornis and in 1955 he recorded that the species was virtually exterminated on his Juncus squarrosus site at Moor House. He was able to correlate this with a very dry period in July when he recorded a mean 'relative humidity' for the surface peat of 3.20 (R.H. = water content of peat/dry weight of peat). It is perhaps unfortunate

that no such drought has occurred during the period 1964 to 1970 which is covered by the M.ater study, as this would have provided some valuable knowledge about the role played by desiccation.

The ratio Rainfall/Potential Evaporation, both of which are measured at Moor House, provides a good indication of the wetness of the moor (Green 1959). During the study this value has only twice dropped below unity, indicating an excess of potential evaporation over rainfall, and therefore a drying of the ground. These two occasions were in June 1967 and July 1969 and each time the ratio was 0.9. In May 1970, at the end of the study, the ratio was 0.8 and in June 1970 it was 1.0, but observations continued into 1971 have not indicated any excessive mortality that could be attributed to this relatively dry spring. The measurements to permit a calculation of the rainfall:evaporation ratio were not made at Moor House in 1955, but measurements of 'relative humidity' of the peat in 1967 permit a comparison with the 1955 situation and indicate that in 1967 at least, the moor did not dry out to the extent that it did in 1955. In June 1967 the mean 'relative humidity' of the top 4cm of the peat from the Podsol and Gley sites was 4.73, a value about midway between the 3.20 recorded by Coulson in July 1955 and 6.08 recorded in November 1955 when the moor was waterlogged. It is therefore not surprising that the life tables for both sites show a fairly constant percentage mortality for the egg and first instar stages, although it has been noted earlier that 1969 was the year of minimum density at the Podsol and Gley sites.

5.7.4 Predators

With eggs of mean length 221μ and first instar larvae of mean length about 0.5mm, it is thought that predation from harvestmen and spiders may be discounted.

Banage (1963) has shown free living nematodes to be very abundant on J.squarrosus at Moor House during the summer, with population densities about 2 million per sq.m. One family, the Mononchidae, is definitely predatory and has been known to take Enchytraeidae, so it is reasonable to assume that they could prey upon the eggs and first instar larvae of M.ater. However, this family comprises a small proportion of the population that is never greater than 1%.

Mesostigmatic mites, which may also be predatory, have been recorded by Block (1965) to have a mean annual density (per sq.m $\pm$ SE) of 2550 $\pm$ 300, on J.squarrosus at Moor House. However, the prey of these species is not known.

Hadley (1966) stated that examination of many hundreds of larvae failed to reveal any sign of either internal or external parasitism. The carnivorous larvae of Tricyphona immaculata have been observed to eat M.ater in the laboratory, but if enchytraeid worms were included in the culture, the M.ater larvae were not taken. However, Hadley was undoubtedly studying the later instars if M.ater and the preference for Enchytraeidae might have represented a preference for a smaller size of prey. The density of T.immaculata during the present study has been in the order of

200 per sq.m in the spring. This species has two generations each year at Moor House and the numbers of larvae large enough to be predatory on M.ater eggs and first instar larvae during June and July is not known.

No information is available on the densities of other Diptera or Colelptera that might be predatory here.

5.7.5 Fecundity

Although in the foregoing analysis the reduction in fecundity has been considered operating within the adult population, the earlier consideration of this topic has shown that it can be traced back to the larval feeding stage in the spring.

The existence of a density dependent reduction in fecundity has been demonstrated at both the Podsol and Gley sites. The slope of the regression of log density of maximum fecundity females on log density of females is 0.75 at the Podsol and 0.77 at the Gley site. The closeness of these values indicates that the limiting factor is operating to a similar extent at both sites. However, these slopes are higher than those for the egg density on instar two regression, indicating that the regulation brought about by reduction of fecundity is less than that due to predation of eggs and first instar larvae. Given that this latter, highly regulatory mortality, immediately follows the reduction of fecundity, it is difficult to see that the

density dependent reduction of fecundity has much importance in the regulation of the population numbers.

5.7.6 Other causes of mortality

The key factor analyses have indicated that, with the exception of egg and first instar mortality, the other age interval mortalities are relatively unimportant in the population dynamics of M.ater. When individual sites and years are considered in detail one or two divergences from the general trend may be seen. Thus the pupation and emergence mortality, k_6, was particularly high in 1969 at the Podsol site, this one event bringing it into consideration as a secondary key factor. A high k_6 mortality is not consistently found throughout the rest of the data in 1969 and its occurrence at the Podsol site cannot be explained. Nevertheless it probably contributed to the low adult density in 1969.

A low adult density was also recorded in 1969 at the Gley site, but inspection of Figure 36 shows that it was not due to a high pupation and emergence mortality although the high overwinter mortality is important here.

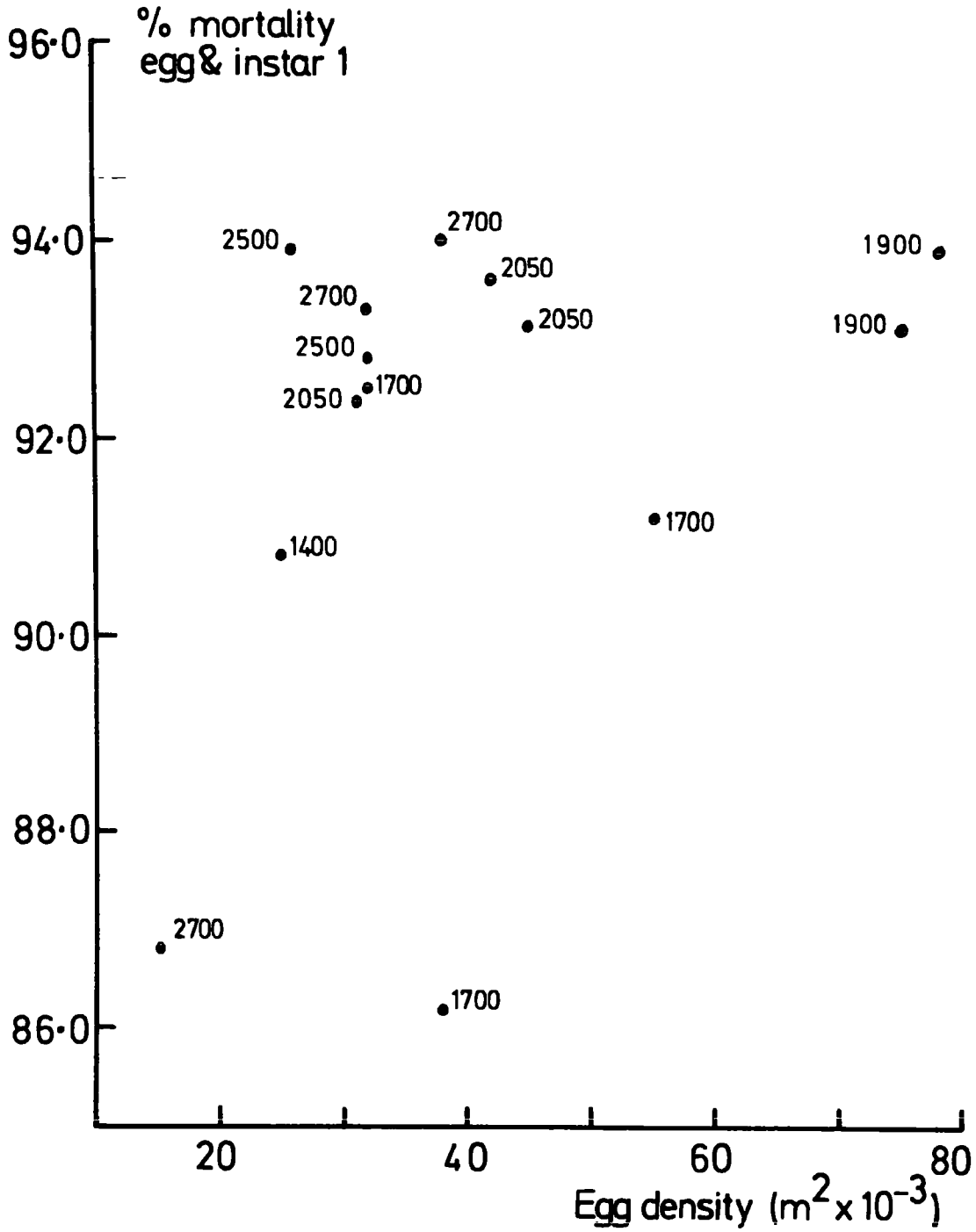
Overall there is little to be gained by a detailed consideration of such fluctuations in mortality at individual sites when insufficient is known about the precise climatic and biological conditions that prevailed there. One advantage of the key factor analyses is that they permit the important parameters of the overall situation to be identified, and it is these that would repay more intensive study.

5.7.7 Population data from other sites

The population densities recorded at the 1400', 1700', 1900', 2050', 2500', and 2700' sites on Dun Fell, together with those from the Blanket Bog site, are presented in life table form in the appendix. All the sites indicate a survivorship curve of the Slobodkin type IV. The key factor analyses that have been presented earlier demonstrated the existence of a density dependent component in the egg and first instar mortality, and a similar effect can be seen in the data from the Dun Fell sites. In Figure 37 the percentage mortality of egg and first instar is plotted against egg density. There is no reason to expect the different sites to be strictly comparable, but when either all of the data or just that belonging to one site is considered, there is obvious evidence of a general increase in percentage mortality with increasing egg density. Inspection of the Blanket Bog life table is sufficient to show that the same density dependence exists here, although the Blanket Bog densities are much lower.

It is thought that the density dependent mortality is acting here in conjunction with a density independent factor that has been suggested in the earlier analysis to be primarily due to desiccation. The separate effects of the two factors cannot be known with information at present to hand; indeed, the action of the density dependent factor would be such as to mask any differential mortality due to varying wetness, except under conditions of extreme drought. This is illustrated in Figure 38

Figure 37. The percentage mortality of the M.ater eggs and first instar larvae in relation to the egg density at the Dun Fell sites.

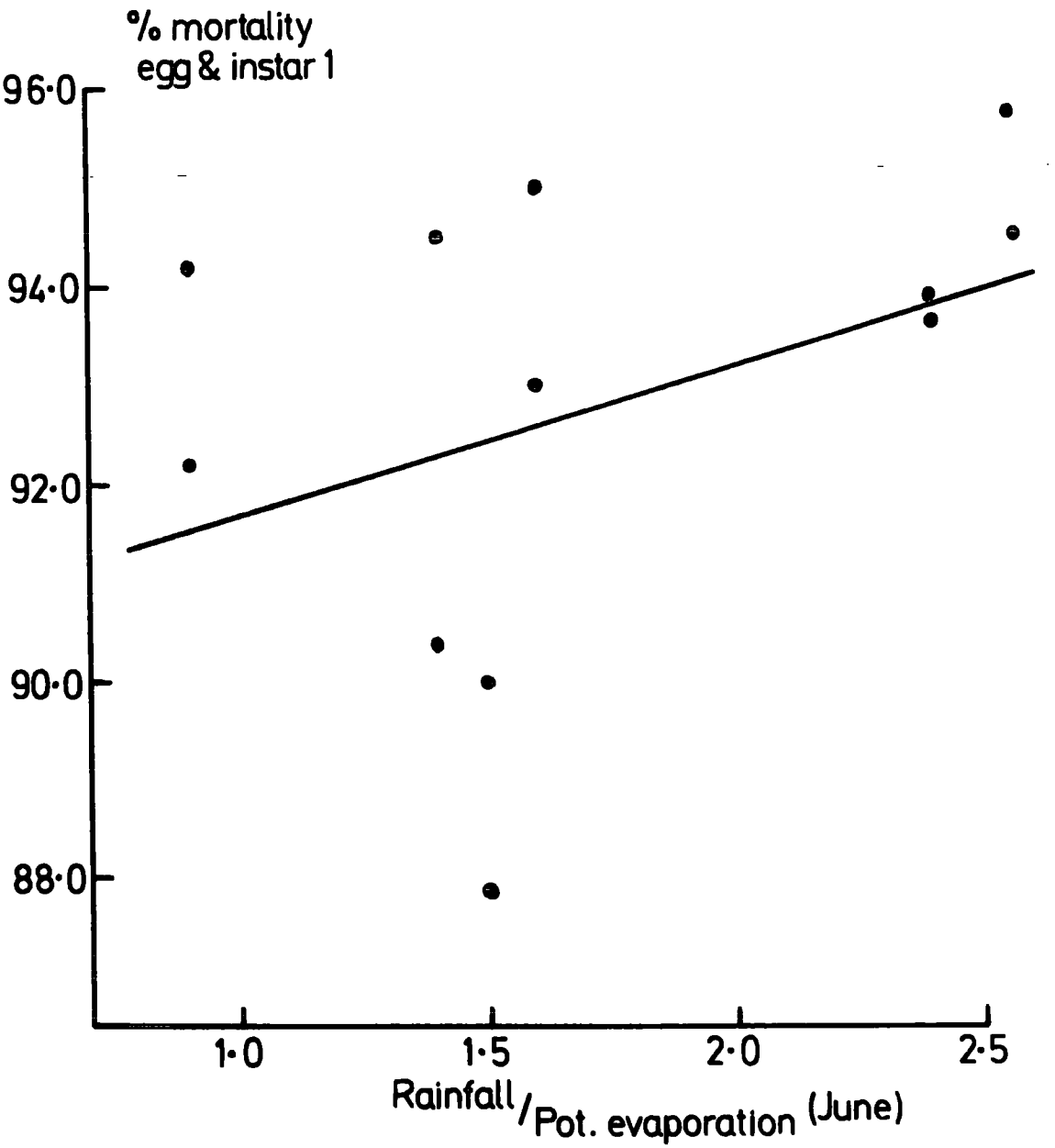

% mortality
egg & instar 1
96·0
94·0
92·0
90·0
88·0
86·0
2500
2700
2050
2700
2050
2500
1700
2050
1900
1900
1700
1400
2700
1700
20
40
60
80
Egg density (m² x 10⁻³)

where the percentage egg and first instar mortality at the Gley and Podsol sites is plotted against the ratio of Rainfall/Potential Evaporation for June over the period 1964 to 1969. The ratio gives some indication of the dryness of the soil, and June is the month when most of the mortality due to desiccation is thought to occur. The regression line of $y = 90.2 + 1.5\,x$, whose slope is not significantly different from zero, $t = 1.375$, $P = 0.2$, shows that there is no tendency for either a consistent increase or decrease in mortality, with a change in the R/PE ratio.

The percentage mortalities that have been very tentatively ascribed to desiccation and predation give no information about how many eggs and larvae actually die due to each cause. It is clear that a 39% mortality, acting immediately on the maximum number of eggs in the soil, will produce more deaths than the same percentage mortality acting later on much reduced numbers. The most reasonable hypothesis is that both mortalities occur synchronously during June and July, with the possibility that desiccation mortality reaches peaks during particularly dry spells in June that may last for only a few days.

Once the eggs are hatched it is likely that the positive hydrotaxis and negative phototaxis that have been observed casually from larvae in culture would serve to minimise desiccation mortality, except

Figure 38. The relationship between the percentage egg and first instar mortality, and the rainfall/potential evaporation (R/PE) ratio at the Peaty Gley and Peaty Podsol sites, 1964 - 1969. The equation of the line is $y = 90.2 + 1.5x$ and the slope is not significantly different from zero, $t = 1.375$ $df = 10$ $P = 0.20$.


% mortality
egg & instar 1
96·0
94·0
92·0
90·0
88·0
1·0
1·5
2·0
2·5
Rainfall / Pot. evaporation (June)


19 MAY 1971
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in conditions of drought, which it has been noted earlier have not occured at Moor House between 1964 and 1970. However, the movement of the larvae into the upper 3cm layer of the soil would bring them into the zone at Moor House, which Block (pers.comm.) has found to be occupied by 95% of the mites.

The effect of the population regulation has been summarised by calculating the coefficient of variation $\left(\frac{\text{Standard deviation x 100}}{\text{Mean}}\right)$ for the densities at the egg, instar two, instar four (November - December), and adult stages, for all the Juncus squarrosus sites from the data presented in the appendix. The coefficients of variation are : 40.0%, 35.8%, 35.1%, and 48.5%, respectively. The most variable is the adult stage, occurring immediately prior to the operation of the two regulating mortality factors in the life cycle of M.ater, namely, reduction in fecundity, and egg and first instar mortality. At the Gley and Podsol sites, which were considered in detail earlier, reduction in fecundity was thought to be of reduced importance as a regulator, compared with egg and first instar mortality, but the reduction of 8.5% between the coefficients of variation at the adult stage and at the egg stage may indicate otherwise, compared with the reduction of 4.9% between the coefficients of variation at the egg and second instar stages, which is due to the regulating effect of egg and first instar mortality.

5.7.8 Overwinter Mortality

Overwinter mortality was not found to be important at the Gley or the Podsol sites, either in the contribution to variation in mortality from year to year, or in a density dependent, regulatory sense. What most characterises this mortality is its variation within the same site in different years. Thus, at 1700', the lowest overwinter mortality was 15.8% in 1967-68 and the highest was 58.8% in 1969-70, while at 2700' the lowest overwinter mortality was 22.4% in 1967-68 and the highest was 30.0% in 1968-69. An inspection of the life tables indicates that changes in density cannot account for this variation.

It was thought that overwinter mortality might show some relation to altitude, with the colder temperatures producing higher mortalities. This is not so, and in Table 64 the average overwinter mortality for the three years 1967-70 is given for each site.

Table 64 shows that there is clearly no tendency for the higher altitude sites to produce a greater mortality during the winter. However, as the temperature data presented in Section 3 have shown, during the winter the temperature differences between the sites are at a minimum and so the absence of any obvious trend, particularly over the short period of three generations that has been studied, may not be conclusive.

TABLE 64. Average overwinter mortality 1967 to 1970

Site	Average Overwinter Mortality
Podsol	11.0%
1900'	17.7%
Gley	24.8%
2700'	26.0%
Bl.Bog	29.4%
1700'	34.0%
2050'	46.6%

No detailed information on the cold hardiness of M. ater larvae has been obtained, but they can survive inside frozen soil in the field, and at temperatures below 0°C in the laboratory. However, during the winter and spring of 1967 some investigations into the cold hardiness of the overwintering, third instar larvae of Tipula paludosa were performed.

Larvae were cultured at a variety of constant temperatures and were then placed at different sub-zero temperatures for ten hours. After this they were allowed to return to the culture temperature over a period of a few hours. Larvae were always maintained at any one culture temperature for at least a week prior to being placed at a low temperature. Some larvae were used more than once in the experiments. The details of the temperatures and the results are given in Table 65. During each experiment a control group was maintained at the culture temperature, and no deaths were recorded among these controls.

TABLE 65. The Percentage of larvae surviving cold hardiness experiments with Tipula Paludosa

Culture Temp. °C	Cold Regime (10 hours)	No. Larvae	% Surviving
6.0	-2.0	15	100
6.0	-4.0	13	100
6.0	-6.0	10	0
15.0	-4.5	9	0
10.0	-4.5	9	11
6.0	-4.5	9	100
2.0	-4.5	9	100
6.0	-6.0	10	0
2.0	-6.0	6	33

The results in Table 65 demonstrate the ability of these T.paludosa larvae to survive sub-zero temperatures, and also demonstrate cold acclimatisation since a lower culture temperature decreases the low temperature that the larvae can survive.

The applicability of these results to M.ater is open to question, but it does seem clear that the species survives equally well over the 1400' to 2700' altitude range that has been studied here. Extended observations to determine under what climatic conditions M.ater begins to be restricted would be particularly interesting.

6. GENERAL DISCUSSION

The climate of the Moor House National Nature Reserve has been described by Pearsall (1956) as typical of the montane regions of Britain, and by Manley (1936) as sub-arctic, having many features comparable to those at sea level in Southern Iceland. Manley was, however, concerned with the meteorology of this Pennine area, and his conclusions were based on temperature measurements taken within a standard Stevenson Screen at a height of 1.5 metres above the ground, together with the standard gauge for measuring precipitation.

Such measurements are of fundamental importance in that it is the basic meteorological parameters of air temperature, wind, precipitation, and sunshine that subsequently contribute to the environmental climate of any organism. To the biologist the problem remains of interpreting these data. For a general comparison of some biological event with an aspect of an organism's climate it is sufficient to use this basic meteorological data when large climatic differences are involved. The effects of periods of abnormally cold weather have been described by numerous authors, one of the most recent being Crisp et al (1964) who have described the severe effects of the cold winter of 1962-63 on the marine and littoral fauna of Britain. Bro Larsen (1944), Nielson (1955), and Springett (1967) have shown that various members of the soil fauna may suffer heavy falls in their population densities during cold winters.

Coulson (1962) has shown the effect of a summer drought on a species of moorland crane-fly. Rainfall and potential evaporation data, taken from the Moor House meteorological records, have been used in this thesis to indicate the dryness of the soil, particularly in relation to excessive desiccation mortality occurring under dry conditions.

Macfadyen (1964), however, has pointed out that the climate in which animals actually live is very different from that measured by the meteorologist, and it is obvious that a more detailed investigation is necessary in order to understand the climate surrounding a crane-fly larva living in the top 6cm of the soil. There are two approaches towards this understanding. The first involves the prediction of the soil climate from the conditions measured above the ground. Coutts (1955, 1958) has presented temperature measurements of a forest soil in Aberdeenshire, and has considered the validity of estimating both the mean air and soil temperatures from "spot readings" of temperature, which are often all that are available from small meteorological stations. Where only one reading, often at 09.00 hrs, is taken, errors in the order of one to two degrees centigrade occur in attempts to estimate the mean air temperature. A maximum and minimum reading of air temperature each day permits a better estimate of the mean air temperature, although Macfadyen (1956) has shown that the median of these values, i.e. $\frac{1}{2}$ (max + min), produces an estimate that is lower than the true mean in the summer, and higher than the true mean in the winter.

This is because the prolonged daylight period in the summer produces temperatures above the median value of the maximum and the minimum, while the short daylight period in the winter has the reverse effect.

Accepting this limitation, Coutts (1958) showed that 69% of the estimated mean air temperatures fell within the range $\pm$ 0.5°C of the true mean air temperature, and 89% of the estimated soil temperatures at one inch depth fell within the same range of true mean soil temperature. A similar relationship derived during the present study gave much less accurate estimates of soil temperature, and this was probably due to the greater variation of both the vegetation and the climate. Rain storms have been shown by Geiger (1951) to change the soil temperature very rapidly, and such storms are frequent at Moor House, while Coutts (1958) noted the large measure of rain interception by the forest canopy.

The insulating effect of snow cover on soil temperature has been considered by several workers (Franklin 1920, Oke & Hannell 1966). The most fundamental work on the relationship between ground and air conditions is that of Geiger (1951) whose work shows the obvious limitations of the predictive approach. So many factors, such as aspect, latitude, time, atmospheric conditions, surface cover, and soil, are involved in the determination of soil temperature that it is usually easier to measure the temperature directly.

It is small changes in any of these parameters that produce the climatic variability in an apparently

uniform habitat, and the problem of accounting for these different microclimates is a difficult one. It is often necessary to make a subjective judgment of the accuracy to which measurements are to be made, based on biological knowledge of the animal under study, and to this extent the definition of what constitutes a microclimate can vary from study to study.

Many authors have adopted the second approach of the direct measurement of both above and below ground temperatures, using a variety of methods (Cloudsley-Thompson 1965, Ludwig & Harper 1958, Pryor 1962, Oke & Hannell 1966, and Healey 1967). All have noted that the deeper soil layers are more equable than the surface areas, and that there is one position, either at the soil surface or above it where the highest daytime and lowest night-time temperatures occur. This is the "outer active surface" of Geiger (1951), and represents the surface at which absorption of the sun's radiant energy occurs, and from which it is mainly radiated. This may be the ground surface, or some position in the aerial vegetation, depending on the density of the latter.

Healey (1967) recorded weekly mean temperatures using the thermistor and silver voltameter technique described by Macfadyen (1956), and found the most variable range of temperature to be at the litter surface, underneath Bracken (Pteridium aquilinum (L) Kuhn) which he described as patchy and of rather stunted growth. At an altitude of 500' he found an annual mean temperature, for the top 3cm of the soil, of 9.3°C, and showed differences in

annual mean temperatures of up to 1.7°C between sites only six metres apart, but with different vegetational cover. The mean annual temperature at 2780' on Great Dun Fell was found in the present study to be 4.1°C, and at the lowest site, 1200' on Great Dun Fell, it was 6.4°C. These results are proportionately lower than the value of 9.3°C obtained by Healey, but his study was of a moorland area in South Wales where higher temperatures might be expected. His differences in the mean annual temperatures between adjacent sites are a warning against the over generalisation of soil temperatures, and his value of 1.7°C quoted above may be compared with the 2.3°C difference in mean annual temperature between the 2780' and 1200' sites on Great Dun Fell. A difference of 1.1°C was obtained at the same altitude in the present study, between the mean annual temperatures at the Above Netherhearth and Peaty Podsol sites at Moor House, although the warmth of the latter is partly due to a slope of southerly aspect.

It is important to remember here that it is the temperature of the animal's surroundings, in the above example the soil, that is being measured and not the temperature of the animal itself. For soil animals it is probably reasonable to assume that these two parameters are identical, particularly in the very wet conditions that have existed in the present study. Any consideration of the effect of temperature on the adult crane-flies, or any other above ground poikilotherms, would need to take this distinction into consideration, for as Parry (1951a, 1951b) has shown, the temperatures recorded inside metal models,

which correspond fairly well with the temperatures recorded inside the bodies of locusts, depend largely on size, colour, shape and orientation, and can be very different from the recorded air temperatures under conditions of direct sunshine. Waterhouse (1951) has shown that variation in the saturation deficit of the air surrounding Lepidoptera and Hymenoptera larvae can produce marked changes in the temperature recorded inside the bodies of the larvae. A similar effect was recorded inside a piece of clay of similar size and shape, and Waterhouse concluded that the temperature differences were due largely to evaporation and condensation at the outer surface of the larval integument.

Research on the temperature relations of insects can be divided into two main categories. The first concerns a delimiting effect, where temperature determines within what range an insect can survive, the upper and lower lethal limits, together with intermediate temperature thresholds which can control development from one stage of the life cycle to another. The second category concerns the effect of temperature on metabolism, viewed as a whole in its manifestations as growth or movement, for example, or as specific biochemical reactions. It is at this latter level that the distinction between the two categories breaks down, when, for example, a temperature threshold can be shown to be due to failure to produce a known hormone.

An immense amount of work has been published on the temperature tolerances of insects. The early research has been summarised by Uvarov (1931), and Mellanby (1939), who has investigated insect activity at low temperatures,

defined the cold death point as the temperature below which exposure was lethal, and the "chill coma temperature" as the temperature at which the insect was immobilised by cold. He thought that the latter was the most important factor limiting insect distribution in the temperate regions, where conditions are seldom sufficiently extreme to kill many insects, but species might often be prevented from active life or breeding by low temperature. The climate at Moor House, however, is sub-arctic, not temperate, and an ability to survive periods of sub-zero temperature is probably the more important factor here. Mellanby found that the past history of the insects used in his determinations of the chill coma temperature was most important, and he demonstrated that acclimatisation effects with respect to the chill coma temperature usually occured within twenty hours. He also tentatively concluded that acclimatisation to chill coma temperature was accompanied by a similar acclimatisation of the cold death point. The work of Mellanby has been extended by Colhoun (1960) who found that there was a temperature below which further acclimatisation is not achieved.

Mellanby (1940) in a study on the activity of some arctic insects found that his results could be divided into two classes. One group, which included the later stages of a stone-fly and the adults of a mosquito, showed evidence of acclimatisation of their chill coma temperature that enabled them to remain active at $0^{\circ}C$. The other group, which included the nymphs of the stone-fly and larvae of the mosquito, were always active at $0^{\circ}C$,

irrespective of their acclimatisation temperature. Mellanby thought that this latter group would still show acclimatisation effects if they could have been cooled below 0°C, and he noted that these were the stages likely to be subjected to prolonged periods of low temperature during the winter, to which the adult stages, which only appear later, are not subjected.

Such a situation might well occur amongst the Tipulidae at Moor House for although no acclimatisation studies on the adults have been carried out, the investigations reported earlier on the overwintering larvae of Tipula paludosa have demonstrated the acclimatisation of their lower lethal limit to temperatures several degrees below 0°C.

Lethal and coma temperatures are just extreme thresholds that delimit the temperature range within which the insect can live. Many authors have considered the variety of thresholds that can exist at the different stages of an insect's life cycle. Wigglesworth (1950) has reviewed this subject and has given examples of minimum temperatures that must be exceeded before, for example, moulting or flight can occur. Johnson (1940) has demonstrated the need for considering the existence of various finite thresholds, and Hodson & Al Rawy (1958) have considered temperature in relation to developmental thresholds in insects. Richards (1964) has suggested that two general relationships appear to hold with respect to the eggs of a variety of insects. One is that the rate of oxygen consumption, expressed as a natural logarithm,

has a linear relationship to the reciprocal of the absolute temperature, while growth rate on the same Arrhenius-type plot gives a downward curve. The point at which the growth rate falls steeply with very little decrease in temperature is taken as the temperature threshold for the development and hatching of the eggs to produce viable larvae. Richards suggested that the temperature threshold for successful hatching represents the temperature above which some essential biological event can only occur, but this postulated event has not been recognised.

In addition to the temperature threshold for the hatching of viable larvae, Richards has given several other temperature thresholds that occur in the development of the egg of the bug Oncopeltus fasciatus (Dallas). These include 14°C for full embryonic development, 15°C for full development plus hatching, and 18°C for the production of viable larvae. The determination of these thresholds is the result of several years' work at many temperatures and it must remain pure speculation how many such thresholds exist in the life cycle of any insect species.

In the present study it has been suggested that temperature thresholds are responsible for synchronising the life cycles of several crane-flies in the absence of diapause or other well documented threshold parameters such as humidity and photoperiod. Such a synchronising threshold has been thought to operate at the pupation of the crane-fly larvae, a suggestion first put forward by Coulson (1956) and developed in Section 4 of this thesis

where it is thought that a threshold of about 6°C must be exceeded before the fourth instar larvae of Molophilus ater can pupate. This situation has been contrasted with the larvae of Tipula pagana where there may be a maximum threshold below which the temperature must fall before pupation can take place. Such a threshold could easily be imagined as that below which some pupation inhibiting hormone could not be produced. Corbet (1958) has discussed temperature in relation to the seasonal development of several Odonata species and has shown the existence of both maximum and minimum thresholds although these have been mainly in relation to diapause.

The literature describing the effects of temperature on the metabolism and growth of insects is equally vast. The mathematical descriptions of temperature effects have been summarised by Wigglesworth (1950). In the present study it appeared that rate of larval development was directly proportional to temperature, a relation stated by Wigglesworth to hold for the larvae and pupae of many Diptera when the middle of their developmental temperature range is considered. Such a linear relationship breaks down at the extremes of the temperature range in which development can occur and the extrapolation to the temperature at which development falls to zero must be undertaken with caution.

A further well known relationship is that the logarithm of the rate of metabolism is proportional to the temperature. The Q_{10} is the constant value or

temperature coefficient which represents the proportionate increase in the developmental rate over a temperature increase of 10°C. While this relationship holds fairly well for chemical reactions, where the Q_{10} is usually between 2 or 3, the Q_{10} usually decreases progressively as the temperature increases (Wigglesworth 1950). The Arrhenius relationship described earlier is basically similar to this logarithmic one, since through the narrow range of temperature over which insects exist, the reciprocal of the absolute temperature is almost a linear function of the ordinary temperature. The logistic curve has been suggested by Davidson (1944) to describe the relationship between temperature and rate of development in that it can take some account of the retarding effects of high and low temperatures.

These different relationships are mostly approximations and do not themselves represent basic differences between metabolism and temperature. All of them show a basically linear relationship between rate and temperature over fairly narrow temperature limits, and mainly differ when the extremes of the developmental range are approached. Parameters such as the rate of larval development often require experiments conducted over many days or weeks for their determination, and such has been the case in the present study. The measurement of the respiration rate at different temperatures is often performed instead, but care must be exercised in the interpretation of respiratory data. The work of Richards (1964) shows clearly that for many insects

the variation of egg respiration rate with temperature is not the same as that of egg developmental rate.

The ecological specialisations of high altitude insects have been discussed in great detail by Mani (1962, 1968). Although he was in general concerned with altitudes much greater than those found in England, his observations are clearly relevant to the crane-flies in this work. The tendency towards melanism is well known as one of the characteristics of high altitude insects and it is readily apparent that melanism will permit greater warming in direct sunshine. M.ater adults, as the name suggests, are entirely black, except for white halteres, and they are active in the daytime, a factor which was found to be important by Lewis & Taylor (1965) in their consideration of this topic.

Wing reduction, which is also given by Mani as a high altitude characteristic, is found in both the males and females of M.ater and in the females of T.subnodicornis and T.pagana although Coe (1950) notes the existence of a low altitude macropterous form of the latter species, T.pagana holoptera Edwards, from Warwickshire, Sussex, and Hampshire. Byers (1969) has suggested that wing reduction in crane-flies, whose adults live under cold conditions, has probably resulted from the insects' inability to use them in flight, so that natural selection would not act unfavourably on mutant forms in which wing reduction had occurred.

He quoted as a positive advantage the situation found in several species of the genus Chionea where wing reduction and the loss of the indirect flight muscles has permitted the females to produce up to 4% more eggs by extending their ovaries into the resulting space in the thoracic cavity. This situation was also found by Hadley (1966) to exist in M.ater and he drew similar conclusions to those of Byers.

A number of workers have contributed a considerable amount of information on the ecology of the fauna of the Moor House Nature Reserve. Cragg (1961) has summarised the earlier work and made some general observations on the distribution and regulation of animal numbers. The absence of any large amount of predation and the apparent abundance of plant food material led to the suggestion that the harsh climate was responsible for the local depletion or extinction of animal populations, but that when the overall view was taken such fluctuations contributed to the stability of the whole population. Many authors have, to some degree, subscribed to this view. Nørgaard (1956) attributed population fluctuations of Theridion saxatile to destructive weather conditions which seem to act independently of the population size, and Richards (1961) has stated that "at the extreme edge of the range of a species chance will play an increasing part in control." Whittaker (1963) found that Neophilaenus lineatus was limited in its upper altitude range at Moor House by climatic factors and suggested that, after the unfavourable periods which he recorded, the local population was in danger

of becoming extinct unless it survived in favourable 'pockets' created by the heterogeneity of the area. He thought that a succession of years with more favourable conditions would then be necessary to increase the density level to a point where regulating mechanisms might operate again.

The writings of Thompson (1929, 1939, 1956) and Andrewartha & Birch (1954), who have thought that the abundance of animals is controlled by extrinsic factors that are primarily climatic and edaphic in nature, have led to much controversy. In their exposition of the population dynamics of Thrips imaginis the latter authors asserted that "not only did we fail to find a 'density dependent factor', but we also showed that there was no room for one." In opposition to these ideas Nicholson (1954a, 1954b, 1957, 1958) has stated that populations are controlled by density dependent factors, such that as density increases the density induced factors operate to check the increase. Commenting on attempts to explain population changes in terms of weather, Varley (1963) stated that meteorological parameters "can be combined in an almost infinite number of ways and we quickly make a series of retrospective hypotheses which we test one by one. With any luck at all, by the time twenty different hypotheses have been examined, we can find one which looks hopeful and when tested statistically against the null hypothesis it may well give a probability of $P < 0.05$." He thought that the danger of reaching a false conclusion by this method was "quite appalling"

and that confusion about the meanings of commonly used terms such as control, regulation, and competition, had led to the choice of misleading hypotheses and to the controversy about regulation.

Solomon (1964) has used the phrase natural control to include all the effects that contribute to the limiting of the numbers of animals in natural populations, but has stated that only density dependent processes tend to regulate abundance or population density. He further stated "if an increase of population is stopped by some process other than a density dependent one, this may for the time being constitute an aspect of natural control ...., but I do not call it regulation." Klomp (1962) has shown most clearly, using numerical examples, that the regulation of population density by density independent weather factors is not possible.

The situation that has been summarised by Cragg (1961) is not in conflict with either the statements of Solomon (1964) or Klomp (1962). The large changes in density of several moorland animals that are reported by Cragg can be attributed to what Morris (1959) has described as "Key Factor" mortalities which "cause a variable mortality and appear to be largely responsible for the observed changes in population" density in successive generations. Varley (1963) has pointed out that weather may act as a key factor, but it does not regulate the population, in the sense that regulation has been defined by Solomon (loc.cit.), and it is not density dependent. Weather is not a stabilising influence, but exactly the

opposite, since it is the cause of variation in numbers. When such key factors operate alone in a population, extinction may well result, as Klomp (1962) has stated.

However, it is the idea of localised populations that is important in Cragg's concept, for while extinctions do occur, these extinct populations are thought to be replaced by the same species immigrating from more favourable areas. It is these favourable, reservoir areas, being apparently more stable, that are presumably regulated in the Solomon sense, and it is here that the action of density dependent mortality should be detected.

Hadley (1966) found that the populations of M.ater appeared to be relatively constant from year to year, and his observations have been supported by the further density measurements that have been presented in this study. Although no exceptionally harsh climatic conditions have prevailed during the period 1964 to 1970, it is suggested that, unlike Tipula subnodicornis, M.ater is not under any great pressure from the moorland climate. There was an absence of any marked increase in overwinter mortality at the higher altitude sites; neither did these sites support populations of lower density or of reduced weight.

It has been shown in the present study that mortality occurring during the egg and first instar larva stages has a density dependent component that is probably due to predation. A further density independent component, due primarily to egg desiccation and responsible for most of the variation in generation

mortality from year to year, is also thought to act at this stage, though as the two components are contemporaneous, their precise effects cannot be separated. The predation of the eggs and first instar larvae is thought to be the main mortality factor regulating the population density of M.ater, although a density dependent reduction of fecundity has been demonstrated which is thought to act through the food supply of the larvae, limiting their size in the spring. In this competition for food by the larvae the two sexes may be regarded as distinct populations. Only the females show any increase in weight when population density falls. The absence of any weight increase in the males is more likely to be due to their inability to utilise additional food, rather than their inability to compete with the female proportion of the population, and at no time during the study has larval density, at any site, been high enough to lower the weight of the males by any great amount. Though the contribution made by this density dependent fecundity to the regulation of the population is normally fairly small, it could become important under conditions of extreme spring food shortage when competition between the two sexes would occur, and produce proportionately more reduction in the weight of female larvae, and hence adult fecundity, than has been reported in Section 5.

SUMMARY

1. Moorland Tipulidae have been studied on the Moor House Nature Reserve, Westmorland, from 1966 to 1970, with particular reference to a small brevipalp crane-fly, Molophilus ater Meigen.

2. Some of the study sites were situated on the western, scarp, slope of Great Dun Fell at altitudes from 1200' - 2780'. The others were at approximately the same altitude on the eastern side of the summit ridge.

3. Maximum and minimum temperatures recorded by a mercury in steel thermograph showed the reduction in mean soil temperature at higher altitudes of approximately 0.1°C for every 100' increase in altitude.

4. Exceptions to this situation are discussed, particularly in relation to sites of different aspect and soil.

5. A method of chemical temperature integration using a sucrose solution was used and gave mean temperature estimates of precision ± 0.1°C. The coldest site was at 2780' with an average annual temperature of 4.1°C and the warmest was at a Peaty Podsol site (1820') where the value was 6.6°C.

6. The greater range of temperatures recorded during the season 1969-70 are contrasted with those recorded during 1968-69. Overall the higher altitude sites were more equable than the lower ones, which could be associated with prolonged cloud and snow cover at the former sites.

7. The temperature differences between sites were minimised during winter and spring, while during the summer and the autumn divergence of temperature occurred. During December 1969 - January 1970 only a 1.2°C difference existed between the mean temperature at 1200' and 2780', while during July and August 1969 the range was 5.1°C.
8. The temperature data have been used to calculate cumulative day-degree tables above 0°C and the 1525 day-degrees accumulated at 2780' over the period 23 May 1968 to 9 June 1969 may be compared with 2428 day-degrees accumulated over the same period at 1200'.
9. The pattern of adult emergence for Molophilus ater was obtained using emergence traps and a vacuum sampler.
10. The mean date of emergence occurred at significantly different times, at different sites, and on Dun Fell it was generally delayed by an increase in altitude, being approximately two weeks later at 2700' than at 1400'.
11. The emergence was highly synchronised, with the middle 68% of the emergence lasting about 5 days.
12. The possible factors controlling the emergence have been discussed and the transfer experiments described.
13. The transfer experiments indicated that larvae taken from the same site in either January or April would produce adults at significantly different times if transferred to different sites.

14. It became clear that it was the site to which the larvae were transferred that primarily determined their time of subsequent emergence.

15. Culture studies showed that larvae taken from the different sites at the same time took the same length of time to pupate at the same temperature and indicated that they were all at the same stage of development by the onset of spring.

16. There was no evidence of any diapause, but the culture results suggested that a threshold temperature, below which pupation cannot occur, exists around 5 - 6°C.

17. It has been suggested that this threshold is responsible for both the synchronising of the emergence and the delay in emergence at higher altitudes.

18. Data for the emergence of Tipula subnodicornis show its pattern to be similar, although it emerges about one week earlier than M.ater.

19. Emergence data for T.paludosa and T.pagana show that adults emerge earlier in colder situations and this may be due to a maximum threshold temperature for pupation.

20. The identification of Molophilus larvae has been discussed, together with the sampling and extraction techniques for estimating larval densities. A dynamic wet funnel method was used to extract larvae from soil cores, whose densities prior to pupation in the spring varied from approximately 700 to 2000 per sq.m at different sites.

21. Larval development at the different sites has been considered in relation to the site temperature and in both 1967 and 1968 the Q_{10} was less than 2.0.

22. A maximum temperature threshold may exist during larval development towards instar four because this development was delayed in the warmer year of 1967 compared to 1968.

23. An increase in the mean larval weight at any site led to an increase in the mean weight of the subsequent female adults, but the mean weight of the males was little changed.

24. There was no clear relationship between increase in larval weight and mean site temperature owing to great variation in the results.

25. The mean fecundity of the adult females was closely related to their mean weight.

26. An inverse relationship existed between larval weight and density, and hence female weight and larval density. This leads to a density dependent fecundity relationship which may be due to food acting as a limiting factor.

27. Key factor analyses have been presented for the six years' population data on M.ater which are available for the Podsol and Gley sites.

28. Egg and first instar mortality has been shown to be the key factor which accounts for most of the variation in mortality from year to year.

29. The above mortality, together with the reduction in fecundity, is shown to act in a density dependent manner and to contribute to the regulation of population numbers.

30. It has been suggested that, within the egg and first instar mortality, desiccation is acting as the key factor and predation as the density dependent factor.

31. The data from the other sites, considered in the light of the above analysis, indicate a similar situation. Overwinter mortality did not show any relationship to altitude, and it is concluded that M.ater is not under great pressure from the harsh climate.

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* Original not consulted.

APPENDIX

Life Tables for *M.ater*

The life tables comprise the usual three columns :

l nos. living per sq.m.

d nos. dying per sq.m.

100q percentage mortality.

The data have not been corrected so as to start with a fixed number of individuals as this causes the important information on actual population size to be lost.

1. The Peaty Podsol Site

		1964-65			1965-66		
Stage	Time	l	d	100q	l	d	100q
Eggs	June	51000			53500		
			47500	93.1		49400	92.3
Inst.1	July	3500			4100		
			700	20.0		750	18.3
Inst.2	August	2800			3350		
			600	21.4		700	20.9
Inst.3	September	2200			2650		
			200	9.1		100	3.8
Inst.4	Nov-Dec	2000			2550		
			100	5.0		230	9.0
Inst.4	Mar-April	1900			2320		
			34	1.8		120	5.2
Adults	May-June	1866			2200		
			1179	63.2		1390	63.2
Adult ♀♀	"	687			810		
			111	16.2		131	16.2
♀♀ (93)	"	576			679		

Peaty Podsol Site (contd.)

	1966-67			1967-68		
Stage	l	d	100q	l	d	100q
Eggs	63200			47200		
		58700	92.9		41100	87.1
Inst.1	4500			6100		
		1000	22.2		2420	39.7
Inst.2	3500			3680		
		750	21.4		960	26.1
Inst.3	2750			2720		
		150	5.5		300	11.0
Inst.4	2600			2420		
		250	9.6		190	7.9
Inst.4	2350			2230		
		110	4.7		0	0
Adults	2240			2480		
		1664	74.3		1614	65.1
Adults ♀♀	576			616		
		68	11.8		20	3.2
♀♀ (93)	508			596		

NOTE :

1. The Adult, Egg, and first and second instar densities for 1966, at both the Podsol and Gley sites, have been estimated, in the absence of direct measurement.
2. Where a stage shows a higher density than its predecessor, the situation has been taken to indicate no mortality.

Peaty Podsol Site (contd.)

	1968-69			1969-70		
Stage	l	d	100q	l	d	100q
Eggs	55450			35340		
		51050	92.1		30720	86.9
Inst.1	4400			4620		
		1600	36.4		1080	23.4
Inst.2	2800			3540		
		920	32.9		850	24.0
Inst.3	1880			2690		
		30	1.6		150	5.6
Inst.4	1850			2540		
		240	13.0		310	12.2
Inst.4	1610			2230		
		535	33.2		0	0
Adults	1075			2540		
		695	64.7		1580	62.2
Adult ♀♀	380			650		
		0	0		84	12.9
♀♀ (93)	380			566		

2. The Peaty Gley Site

		1964-65			1965-66		
Stage	Month	l	d	100q	l	d	100q
Eggs	June	27600			56000		
			24400	88.4		51650	92.2
Inst.1	July	3200			4350		
			550	17.2		850	19.5
Inst.2	August	2650			3500		
			200	7.5		550	15.7
Inst.3	Sept.	2450			2950		
			300	12.2		150	5.1
Inst.4	Nov-Dec	2150			2800		
			50	2.3		450	16.1
Inst.4	Mar-April	2100			2350		
			142	6.8		250	10.6
Adults	May-June	1958			2100		
			1240	63.3		1365	65.0
Adult ♀♀	"	718			735		
			251	35.0		257	35.0
♀♀ (120)	"	467			478		

2. The Peaty Gley Site (contd.)

			1966-67			1967-68	
Stage	Month	l	d	100q	l	d	100q
Eggs	June	57350			35200		
			52850	92.2		31200	88.6
Inst.1	July	4500			4000		
			2100	46.7		1950	48.8
Inst.2	August	2400			2050		
			850	35.4		700	34.1
Inst.3	Sept	1550			1350		
			150	9.7		300	22.2
Inst.4	Nov-Dec	1400			1050		
			50	3.6		350	33.3
Inst.4	Mar-April	1350			700		
			100	7.4		60	8.6
Adults	May-June	1250			640		
			883	70.6		456	71.3
Adults ♀♀	"	367			184		
			74	20.2		0	0
♀♀ (120)	"	293			184		

The Peaty Gley Site (contd.)

Stage	Time	1968-69 l	d	100q	1969-70 l	d	100q
Eggs	June	22100			17650		
			19600	88.7		14650	83.0
Inst.1	July	2500			3000		
			950	38.0		850	28.3
Inst.2	Aug	1550			2150		
			550	35.5		1050	48.8
Inst.3	Sept	1000			1100		
			0	0		100	9.1
Inst.4	Nov-Dec	1100			1000		
			450	40.9		250	25.0
Inst.4	May-Apr	550			750		
			80	14.5		80	10.7
Adults	May-June	470			670		
			305	64.9		490	73.1
Adults ♀♀	"	165			180		
			18	10.9		30	16.7
♀♀ (120)	"	147			150		

3. The Blanket Bog Site

		1967			1967-68	
Stage	Time	l	d	100q	l	d	100q
Egg	June				18400		
Inst.1	July						
						17500	95.1
Inst.2	Aug				900		
						130	14.4
Inst.3	Sept				770		
						210	27.3
Inst.4	Nov-Dec				560		
						330	58.9
Inst.4	Mar-April	600			230		
			46	7.7		18	7.8
Adults	May-June	554			212		
			377	68.1		132	62.3
Adult ♀♀	"	177			80		

3. The Blanket Bog Site (contd.)

		1968-69			1969-70		
Stage	Time	l	d	100q	l	d	100q
Egg	June	7800			7300		
Inst.1	July						
			7400	94.9		6860	94.0
Inst.2	Aug	400			440		
			90	22.5		90	20.5
Inst.3	Sept	310			350		
			80	25.8		40	11.4
Inst.4	Nov-Dec	230			310		
			38	16.5		40	12.9
Inst.4	Mar-Apr	192			270		
			0	0		10	3.7
Adults	May-June	200			260		
			117	58.5		174	66.9
Adults ♀♀		75			86		

4. The 1400' Site

			1968-69			1969-70	
Stage	Time	l	d	100q	l	d	100q
Egg	June				25000		
						20800	83.2
Inst.1	July	3300			4200		
			1200	36.4		1900	45.2
Inst.2	Aug	2100			2300		
			500	23.8		1330	57.8
Inst.3	Sept	1600			970		
			500	31.3		0	0
Inst.4	Nov-Dec	1100			1050		
			430	39.1		230	21.9
Inst.4	Mar-Apr	670			740		
			50	7.5		2	0.03
Adults	May-Jun	620			738		
			380	61.3		446	60.4
Adult ♀♀	May-Jun	240			292		

5. The 1700' Site

		1967-68			1968-69		
Stage	Time	l	d	100q	l	d	100q
Egg	June	54800			32100		
			48250	88.0		26310	82.0
Inst.1	July	6550			5790		
			2120	32.4		3390	58.5
Inst.2	Aug	4430			2400		
			1260	28.4		440	18.3
Inst.3	Sept	3170			1960		
			1650	52.1		530	27.0
Inst.4	Nov-Dec	1520			1430		
			240	15.8		390	27.3
Inst.4	Mar-Apr	1280			1040		
			56	4.4		40	3.8
Adults	May-Jun	1224			1000		
			872	71.2		620	62.0
Adult ♀♀	"	352			380		

5. The 1700' Site (contd.)

Stage	Time	l	d	100q
Egg	June	38,380		
			31470	82.0
Inst.1	July	6910		
			1600	23.2
Inst.2	Aug	5310		
			1190	22.4
Inst.3	Sept	4120		
			1730	42.0
Inst.4	Nov-Dec	2390		
			1405	58.8
Inst.4	Mar-Apr	810		
			0	0
Adults	May-June	985		
			609	61.8
Adult ♀♀	"	376		

6. The 1900' Site

			1967-68			1968-69	
Stage	Time	l	d	100q	l	d	100q
Egg	June				75300		
						66970	88.9
Inst.1	July				8330		
						3170	38.1
Inst.2	Aug				5160		
						580	11.2
Inst.3	Sept				4580		
						1180	25.8
Inst.4	Nov-Dec	4850			3400		
			1170	24.1		780	22.9
Inst.4	Mar-Apr	3680			2620		
			264	7.2		595	22.7
Adults	May-June	3376			2025		
			2436	72.2		1225	60.5
Adult ♀♀	"	940			800		

6. The 1900' Site (contd.)

			1969-70	
Stage	Time	l	d	100q
Egg	June	78400		
			71320	91.0
Inst.1	July	7080		
			2230	31.5
Inst.2	Aug	4850		
			1000	20.6
Inst.3	Sept	3850		
			870	22.6
Inst.4	Nov-Dec	2980		
			180	6.0
Inst.4	Mar-Apr	2800		
			120	4.3
Adults	May-June	2680		
			1608	60.0
Adult ♀♀	"	1072		

7. The 2050' Site

		1967-68			1968-69		
Stage	Time	l	d	100q	l	d	100q
Egg	June	30900			41900		
			27660	89.5		37800	90.2
Inst.1	July	3240			4100		
			890	27.5		1400	34.1
Inst.2	Aug	2350			2700		
			250	10.6		400	14.8
Inst.3	Sept	2100			2300		
			260	12.4		380	16.5
Inst.4	Nov-Dec	1840			1920		
			870	47.3		800	41.7
Inst.4	Mar-Apr	970			1120		
			150	1.5		20	1.8
Adults	May-June	820			1100		
			496	60.5		647	58.8
Adult ♀♀	"	324			453		

7. The 2050' Site (contd.)

1969-70

Stage	Time	l	d	100q
Egg	June	44800		
			41110	91.8
Instar 1.	July	3690		
			590	16.0
Instar 2	Aug	3100		
			680	21.9
Instar 3	Sept	2420		
			270	11.2
Instar 4	Nov-Dec	2150		
			1090	50.7
Instar 4	Mar-Apr	1060		
			40	3.8
Adults	May-June	1020		
			657	64.4
Adult ♀♀	"	363		

8. The 2500' Site

		1967-68			1968-69		
Stage	Time	l	d	100q	l	d	100q
Egg	June	25600			31500		
			22620	88.3		27040	85.8
Inst.1	July	2980			4460		
			1430	48.0		2190	49.1
Inst.2	Aug	1410			2270		
			0	0		350	15.4
Inst.3	Sept	1550			1920		
			150	9.7		610	31.8
Inst.4	Nov-Dec	1400			1310		
			300	21.4			
Inst.4	Mar-Apr	1100					
			76	6.9			
Adults	May-June	1024					
			700	68.4			
Adult ♀♀	"	324					

9. The 2700' Site

		1967-68			1968-69		
Stage	Time	l	d	100q	l	d	100q
Egg	June	14500			38400		
			11200	77.2		34390	89.6
Inst.1	July	3300			4010		
			1380	41.8		1710	42.6
Inst.2	Aug	1920			2300		
			330	35.9		260	11.3
Inst.3	Sept	1590			2040		
			0	0		440	21.6
Inst.4	Nov-Dec	1610			1600		
			360	22.4		480	30.0
Inst.4	Mar-Apr	1230			1120		
			14	1.1		100	8.9
Adults	May-June	1216			1020		
			812	66.8		660	64.7
Adult ♀♀	"	404			360		

9. The 2700' Site (contd.)

1969-70

Stage	Time	l	d	100q
Egg	June	32000		
			28400	88.8
Inst.1	July	3600		
			1450	40.3
Inst.2	Aug	2150		
			760	35.3
Inst.3	Sept	1390		
			290	20.9
Inst.4	Nov-Dec	1100		
			280	25.5
Inst.4	Mar-Apr	820		
			80	9.8
Adults	May-June	740		
			445	60.1
Adult ♀♀	"	295		